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Phylogenetic placement of pelican spiders (Archaeidae, Araneae), with insight into evolution of the ''neck'' and predatory behaviours of the superfamily Palpimanoidea

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Abstract

Phylogenetic relationships among archaeid spider lineages, as well as the placement of archaeids within the Araneomorphae, present a problem in the systematics of spiders. We investigate these relationships by broadly sampling taxa from the Araneomorphae and superfamily Palpimanoidea, as well as from extant and fossil archaeid lineages. Using parsimony and Bayesian methods we perform a total-evidence analysis that includes 126 morphological characters and over 4000 bases from one mitochondrial and three nuclear molecular markers. Phylogenetic analysis results in a delimitation of the superfamily Palpimanoidea to contain five families: Archaeidae, Mecysmaucheniidae, Stenochilidae, Palpimanidae and Huttoniidae. We also find the extant archaeids, which are restricted to the southern hemisphere, to be monophyletic, with the fossil archaeids paraphyletic. This phylogenetic framework is then used to interpret a novel morphological character, the highly modified and elevated cephalic area and elongated chelicerae (jaws), coupled with prey choice observations in the field and observations of chelicerae movements during predatory attacks. We conclude that the evolution of the elevated cephalic area, which reoriented the chelicerae muscles, led to highly manoeuvrable chelicerae and associated novel prey capture strategies. All members of Palpimanoidea appear to have modifications to the cephalic area, such as a diastema or sclerotization around the chelicerae bases, and furthermore, members appear to have evolved prey specialization.

Archaeid spiders, commonly called pelican or assassin spiders, are cursorial hunters unique in their extreme modification of the cephalic area and chelicerae (jaws), giving them the appearance of a ''neck'' and ''head'' (Fig. 1e,g,h). Their bizarre appearance, unique predatory behaviors, ''living fossil'' status, and endemism in different parts of the southern hemisphere make them a charismatic group that is well known to arachnologists (Griswold, 2003). Whereas most spiders are predatory generalists (Foelix, 2011), archaeids are highly specialized and will only prey on other spiders (Millot, 1948; Legendre, 1961; Wood, 2008). The highly modified cephalic area in archaeids is used to employ a novel prey capture strategy that is unique among spiders (see fig. 1 in Wood et al., 2007). Furthermore, extant archaeids have a highly restricted, seemingly Gondwanan distribution in the southern hemisphere, being found only in Madagascar, Australia and South Africa. Yet, archaeids were first described from three northern hemisphere Baltic amber fossils (Koch and Berendt, 1854) dated to be of mid-Eocene age (Penney et al., 2011; Fig. 1e). It was not until later that the first living archaeid was found in Madagascar (Cambridge, 1881). Since then, many more extant species have been discovered from Madagascar, South Africa and Australia (Forster and Platnick, 1984; Lotz, 1996, 2003, 2006; Wood, 2008; Rix and Harvey, 2011). At the same time, additional fossil species and genera have been described from northern hemisphere Baltic and Burmese amber (Penney, 2003;

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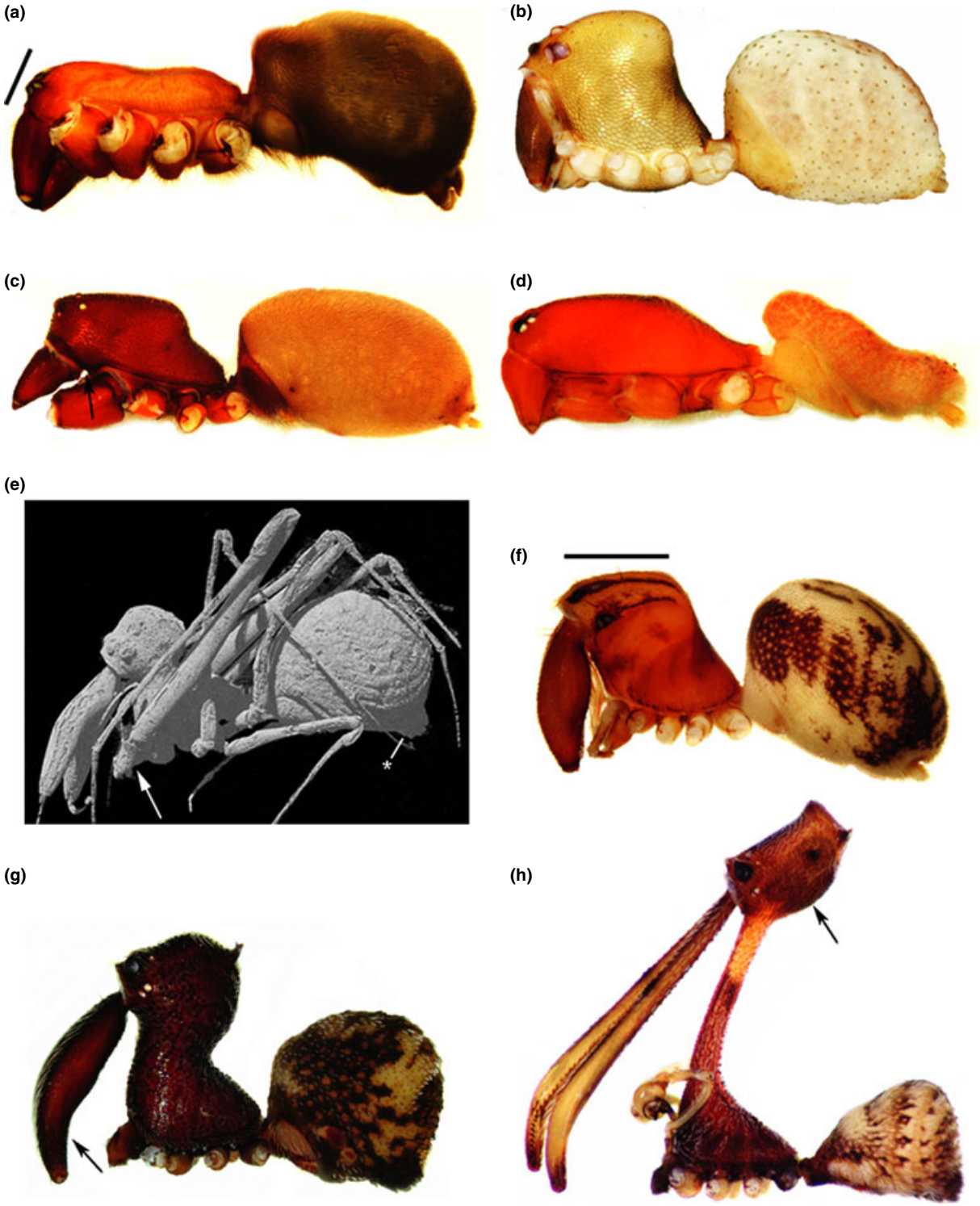

Fig. 1. Lateral view, legs removed, images not to scale. (a) *Hickmania troglodytes*, family Austrochilidae, typical spider body plan without distorted carapace, bar showing approximate orientation of cheliceral muscles; (b) Pararchaeidae spider; (c) *Palpimanus* sp., family Palpimanidae, arrow showing the sclerotized piece between the chelicerae and mouthparts; (d) *Colopea* sp., family Stenochilidae; (e) CT scan of archaeid fossil spider *Archaea paradoxa*, arrow showing long endites, asterisk showing spinneret conical projection; (f) *Aotearoa magna*, a Mecysmaucheniidae, bar showing approximate orientation of cheliceral muscles; (g) archaeid *Afrarchaea woodae*, a species with a short neck, arrow showing curved distal portion of chelicerae; (h) archaeid *Eriauchenius gracilicollis*, the species with the longest neck, arrow showing the rounded out posterior of the cephalic area.

Wunderlich, 2004, 2008), and even compression fossils from Inner Mongolian rocks of Jurassic age (Selden et al., 2008). The enigmatic distributions (fossil versus extant) and unique morphology of these spiders has precluded definitive phylogenetic placement. The current study sets out to address these issues by creating a phylogeny from molecular and morphological data for a diverse array of fossil and extant archaeids, with extensive outgroup sampling that includes a diverse array of taxa representing the major groups of Araneomorphae spiders. Then, using this phylogeny, it examines the evolution of the modified cephalic area (''neck'') from a morphological and behavioural context.

The relationships between the extant and extinct archaeid taxa as well as the phylogenetic placement of the entire family within the distal, higher spiders (the Araneomorphae) have been debated for some years without resolution (Griswold et al., 2005). The suborder Araneomorphae, which comprises the spider families with derived spinning and respiratory organs, contains all the familiar spiders (excluding tarantulas, trap-door spiders and their kin) and makes up the majority of spider biodiversity worldwide (Platnick, 2012). Within the Araneomorphae, families are divided into two genitalic types, the basal haplogynes (or ''simple'' genitalia, with a common entrance for copulation and oviposition) and the more distal, monophyletic, entelegynes (or ''complex'' genitalia, with separate entrances for copulation and oviposition). Archaeids have ''simple'' haplogyne genitalia; their placement within the Araneomorphae is confounded by the issue as to whether they are primitively haplogyne and fall outside the Entelegynae (''complex'' genitalia clade), or whether they are Entelygynae that have secondarily reverted back to the ancestral condition of ''simple'' genitalia.

Reliance on the elevated cephalic area (the ''neck'' and ''head'') as a phylogenetically informative character has served as the basis for historical classifications of archaeid spiders and their closest relatives (Forster and Platnick, 1984). The evolution of a ''neck'' is an unusual trait that is very rare and uncharacteristic of the typical spider body plan (Fig. 1a), yet, whereas this trait is taken to the extreme in archaeids, it also occurs in two other spider families, Mecysmaucheniidae and Pararchaeidae (Fig. 1b,f), whose ''necks'' are shorter and more robust. There are also other spider families that may be intermediate for this trait, such as Holarchaeidae, or that have other modifications to the cephalic area, such as elevated eyes. Based on traits associated with modifications to the cephalic area as well as several other morphological characters, such as presence of a cheliceral gland mound and peg teeth, Forster and Platnick (1984) suggested that Archaeidae (as well as Mecysmaucheniidae and Pararchaeidae) belong to the superfamily Palpimanoidea along with nine other families. This was an expansion of the ''traditional'' Palpimanoidea, which contained only three families, Huttoniidae, Palpimanidae and Stenochilidae. Relationships among archaeid genera and species have in general also been based on traits associated with cephalic modification, such as ''neck'' length (Legendre, 1970; Platnick, 1991). More recently, however, Wood et al. (2007) established that within the Madagascan species the level of elevation, or length, in the cephalic area has evolved in parallel.

Placement of the archaeids requires a broad sample from the Araneomorphae and Palpimanoidea, and inclusion of both molecular and morphological data, as well as fossil archaeids. The current study is the first to generate such a comprehensive data set, including the majority of the families of Forster and Platnick's expanded Palpimanoidea as well as additional families representing major clades within the Araneomorphae. This study addresses three features of archaeid evolution: (i) clarification of the relationships between extant and extinct archaeids by inclusion of several lineages of fossil archaeids; (ii) the placement of archaeids within the Araneomorphae; and (iii) the limits of the superfamily Palpimanoidea and its placement within the Araneomorphae. To this end, we generate a robust phylogenetic hypothesis to reveal the placement of the archaeids and provide insight into the evolutionary history of a novel morphological trait, the modified and elevated cephalic area or ''neck'', across the Araneomorphae. We then use the phylogenetic framework to interpret the evolution of neck morphologies as well as associated predatory behaviours, including prey choice observations and observations of chelicerae movements during predatory attacks.

Materials and methods

Taxon sampling

Currently, in archaeids there are 54 described extant species belonging to three genera, and 18 fossil species belonging to 11 genera, although there are more known extant species still to be described, and more fossil and extant species will probably be discovered in the future. To examine relationships among extant and fossil archaeids we included ten species from Madagascar (five species), Australia (three species) and South Africa (two species), representing the three known extant genera: *Eriauchenius* Cambridge, 1881, *Austrarchaea* Forster and Platnick, 1984, and *Afrarchaea* Forster and Platnick, 1984, as well as the monophyletic ''Gracilicollis Group'' from Madagascar (Wood et al., 2007; Wood, 2008) that is currently placed in *Eriauchenius* (Table 1). Five fossil archaeid taxa were also included, made up of one taxon from Burmese amber [*Burmesarchaea grimaldii* (Penney, 2003) Cretaceous, 88–95 Ma (Penney, 2003)], three taxa from Baltic amber [*Archaea paradoxa* Koch

Table 1
List of vouchers used for gathering morphological data for phylogenetic analysis

Family	Species	Morphology voucher number	Additional sources
Hypochilidae	*Hypochilus pococki*	9034568	Atlas
Filistatidae	*Kukulcania hibernalis*	9025730, 9034584	Atlas
Austrochilidae	*Hickmania troglodytes*	9034570	Atlas
Dysderidae	*Dysdera crocata*	9034577	AToL
Sicariidae	*Loxosceles rufescens*	n/a	AToL
Sicariidae	*Loxosceles deserta*	9034578, 9034579	
Eresidae	*Stegodyphus* sp.	9005868	AToL
Oecobiidae	*Uroctea* sp.	9021405, 9021406	AToL
Araneiidae	*Araneus diadematus*	9034573	AToL
Mimetidae	*Mimetus hesperus*	9034580, 9034581	AToL; Atlas; F&P
Holarchaeidae	*Holarchaea* sp.	9023856, 9023852	AToL
Pararchaeidae	*Ozarchaea platnicki*	9023530	AToL
Pararchaeidae	*Pararchaea alba*	9028408	AToL
Desidae	*Badumna longinqua*	9021775, 9021779	AToL
Gnaphosidae	*Gnaphosa sericata*	9034582	AToL
Lycosidae	*Schizocosa ocreata*	9034571, 9034572	AToL
Palpimanidae	*Palpimanus* sp.	9034583	AToL
Huttoniidae	*Huttonia* sp.	9021410, 9028078	
Stenochilidae	*Colopea* sp.	9035143, 9028424	
Mecysmaucheniidae	*Aotearoa magna*	9028269	F&P
Mecysmaucheniidae	*Zearchea* sp.	9028245, 9028257, 9028253, 9028275	
Mecysmaucheniidae	*Mesarchaea bellavista*	9019105	F&P
Mecysmaucheniidae	*Mecysmauchenius segmentatus*	MACN10284	
Mecysmaucheniidae	*Chilarchaea quellon*	9028089, 9028091, 9034556, 9034519	
Archaeidae	*Eriauchenius lavatenda*	9018944, 9007247	
Archaeidae	*Eriauchenius jeanneli*	9028293, 9015372	
Archaeidae	*Eriauchenius legendrei*	9018992, 9012347	
Archaeidae	*Eriauchenius workmani*	9012335, 9028369	
Archaeidae	*Eriauchenius bourgini*	9028315, 9001207	
Archaeidae	*Afrarchaea* sp.	9028270	
Archaeidae	*Afrarchaea woodae*	9018956, 9018994	
Archaeidae	*Austrarchaea nodosa*	9028426, QMB-S30820	
Archaeidae	*Austrarchaea daviesae*	9034523	
Archaeidae	*Austrarchaea mainae*	9028430, 9028361	
Archaeidae	*Archaea paradoxa*	MB.A1669, SMF-F565	
Archaeidae	*Myrmecarchaea* sp.	GPIH-S3999, GPIH-S3907, SMF-F1132	
Archaeidae	*Baltarchaea conica*	F2171	CT X-ray scans
Archaeidae	*Afrarchaea grimaldii*	AMNH-Bu-256	
Archaeidae	*Patarchaea muralis*	Examined published images	Selden et al. (2008)

In some taxa morphological data also came from additional sources listed here. Unless otherwise specified the voucher number is from the California Academy of Sciences Entomology Department (CASENT); AMNH = American Museum of Natural History; AToL = Assembling the Tree of Life Spider Project; Atlas = Griswold et al., 2005; F = Joerg Wunderlich private collection voucher code; F&P = Forster & Platnick, 1984; GPIH = Geologisch-Paläontologisches Institut der Universität Hamburg; MACN = Museo Argentino de Ciencias Naturales; MB.A = -Museum für Naturkunde Berlin, Paläontologisches; QMB = Queensland Museum, Brisbane; SMF-F = the Senckenberg Museum (SMF) recently acquired the private collection of J. Wunderlich, and these specimens have not yet received SMF voucher numbers so the previous voucher numbers of J. Wunderlich are listed.

and Berendt, 1854, *Baltarchaea conica* (Koch and Berendt, 1854) and *Myrmecarchaea* Wunderlich, 2004, all Eocene–Lutetian, 44–49 Ma (Penney et al., 2011)], and one compression fossil from Inner Mongolian rocks [*Patarchaea muralis* Selden et al., 2008, Middle Jurassic (Chen et al., 2004; Gao and Ren, 2006), 161–176 Ma (based on http://www.geosociety.org/science/timescale/)]. The included fossil taxa represent five of the 11 fossil archaeid genera (Dunlop et al., 2011) [see Selden et al. (2008) for a discussion of archaeid fossils]. The remaining six archaeid fossil genera were omitted from the study subsequent to examination for the following reasons: the genus *Eoarchaea* Forster and Platnick, 1984, has been erected from juvenile specimens and no adult specimens are known (also noted by Eskov, 1992); two *Saxonarchaea* Wunderlich, 2004, specimens were examined and the inclusions were obstructed, preventing examination of important morphological traits; *Filiauchenius* Wunderlich, 2008, is known from one specimen that is highly obstructed by cloudy, discoloured amber; *Eomysmauchenius* Wunderlich, 2008, is known from only one specimen that is highly distorted; *Lacunauchenius speciosus* Wunderlich, 2008, is known from one specimen that is also distorted, making it very

difficult to determine whether many of the suggested morphological traits were real or artefacts of preservation (see Appendix 6 for discussion on this enigmatic taxon); and *Jurarchaea* Eskov, 1987, is too poorly preserved to be identified as an archaeid (also noted by Wunderlich, 2004; Selden et al., 2008).

The remaining five fossil taxa used for this study are all adults, with the exception of *Myrmecarchaea* sp., which consists of a few specimens from two species (*M. petiolus* Wunderlich, 2004, and *M. pediculus* Wunderlich, 2004) that all appear to be juveniles. *Myrmecarchaea* was included in this study because the morphology was preserved well enough to score for somatic characters even though genitalic data were lacking. Specimens representing both adult males and females were present only in the fossil *Archaea paradoxa* whereas in all other fossils one sex was missing. Thus, because it was not possible to score fossil taxa for internal or microscopic characters, and due to lack of molecular data for fossil taxa, the character sets for the fossil taxa are highly incomplete. However, archaeids possess a number of somatic features that are easy to see with a dissecting microscope and through the use of computed tomography scans, and for this reason it was still possible to score the fossil taxa for many characters. Studies have shown that taxa missing partial data are still useful for interpreting homology among characters, and that they do not necessarily create inaccuracies in the phylogeny, and that although inclusion of taxa with partial data matrices may reduce resolution, the inclusion of such taxa may also improve accuracy (Wiens, 2003a,b; Driskell et al., 2004; Philippe et al., 2004; Santini and Tyler, 2004).

We included an additional 22 non-archaeid taxa representing 18 families, with the most basal Araneomorphae family Hypochilidae as the outgroup (Table 1). These additional taxa represent the major clades within the Araneomorphae (Griswold et al., 2005): we intend to avoid biasing the outcome by restricting possibilities, and therefore give archaeids several different places to fall within the Araneomorphae. Furthermore, all family members of Forster and Platnick's (1984) Palpimanoidea were included in the study with the exception of the Micropholcommatinae (considered Micropholcommatidae by Platnick, 2012, but see Lopardo et al., 2011, who placed these as a subfamily of Anapidae) and Malkaridae. It has previously been shown that these families group with members from the superfamily Araneoidea (the orb-weavers and their relatives; Schütt, 2000, 2002; Rix et al., 2008; Dimitrov et al., 2012) rather than with the Palpimanoidea.

When possible we used non-chimeric taxa, but for some species this was not possible because we were limited to assembling terminals from a variety of sources. Of the few taxa that are chimeras, there is no question about the monophyly of the family they are representing; for example, the specimens representing the families Pararchaeidae, Gnaphosidae and Lycosidae are assembled from two different genera, yet the classification of these families is not controversial (Pararchaeidae: Rix, 2006; Gnaphosidae: Platnick, 1990; Lycosidae: Griswold, 1993). Including archaeids, there are a total of 37 ingroup taxa and data for all molecular and morphological vouchers are presented in Tables 1 and 2. We were able to obtain data from four molecular markers (for only the extant taxa) and for 126 morphological characters across a wide range of taxa spanning the Araneomorphae.

Morphological character acquisition

Many of the 126 morphological characters (Appendix 1) were formulated specifically for this study and because the focus of this study is the placement of archaeid spiders, many of these new characters deal with archaeid traits, for example spines on the carapace, scopulae presence and peg-teeth shape. The remaining characters are based mostly on Griswold et al. (2005) and are characters commonly used in spider systematics. The 126 characters deal with genitalia, spinnerets and somatic traits; the morphological matrix is presented in Appendix 2. For some taxa, the morphological character states were scored using data from other studies (Forster and Platnick, 1984; Griswold et al., 2005) as well as from SEM images acquired from other arachnology labs as part of the NSF Assembling the Tree of Life—Spiders project (http://www.morphbank.net, keyword = SpiderAToL).

Morphological data were gathered using a Leo 1450VP (CarlZeiss, Oberkochen, Germany) scanning electron microscope (SEM; for only the extant taxa) and a Leica MZ12.5 (Leica Microsystems, Wetzlar, Germany) stereomicroscope (for both the extant and fossil taxa). Acquiring morphological data required making detailed dissections of the genitalia and the chelicerae and removing body parts for imaging in the SEM. Male genitalia (palps) were further examined by being boiled in lactic acid then placed in ethanol, which caused the palps to expand. Vouchers used for morphological character acquisition are presented in Table 1. When possible, one voucher of each sex was selected per taxon and used for scoring the majority of the characters. Regarding fossil data, over 75 archaeid amber fossil specimens were borrowed from museums and from these, vouchers were selected. Additional specimens were occasionally needed for scoring a fossil taxon when a body part was obstructed or distorted (also listed in Table 1). Three fossil taxa were additionally examined by computed tomography scanning, which was performed at the High Resolution X-ray CT Facility at UT, Austin. Four scans were performed representing three taxa: a male and female *Archaea*

Table 2.
List of vouchers used for gathering molecular data for phylogenetic analysis.

Family	Species	DNA source—voucher code	DNA sequence	GenBank accession no.
Hypochilidae	*Hypochilus pococki*	GenBank—Starrett and Waters (2007); Wheeler and Hayashi (1998);	COI, 28S, 18S	EF537064, AF062977, AF062951
Filistatidae	*Kukulcania hibernalis*	Present study—9034219; extraction—0079	COI, 28S, 18S, H3	JX240233, [JX240273, JX240284], JX240253, JX240303
Austrochilidae	*Hickmania troglodytes*	GenBank—Miller et al. (2010)	COI, 28S, 18S, H3	FJ948985, FJ948945, [FJ948862, FJ948903], FJ949025
Dysderidae	*Dysdera erythrina*	GenBank—Arnedo et al. (2009)	COI, 28S, H3	GQ285643, GQ285619, GQ285625
Dysderidae	*Dysdera erythrina*	AToL ARAMA000013	18S	AToL unpublished sequence
Sicariidae	*Loxosceles* sp.	GenBank—Duncan et al. (2010)	COI	GQ279221
Sicariidae	*Loxosceles rufescens*	GenBank—Binford et al. (2008)	28S	EU817780
Sicariidae	*Loxosceles rufescens*	AToL ARAPS000001	18S	AToL unpublished sequence
Sicariidae	*Loxosceles* sp.	AToL ARASP000030	H3	AToL unpublished sequence
Eresidae	*Stegodyphus* sp.	Present study—9028232; extraction—Steg42	COI, 28S, 18S, H3	JX240234, JX240285, JX240254, JX240304
Oecobiidae	*Uroctea durandi*	GenBank—Miller et al. (2010)	COI, 28S, 18S, H3	FJ949021, FJ948980, [FJ948939, FJ948897], FJ949058
Araneiidae	*Araneus marmoreus*	GenBank—Álvarez-Padilla et al. (2009)	COI, 28S, 18S, H3	EU003278, EU003397, EU003342, EU003312
Mimetidae	*Mimetus* sp.	GenBank—Blackledge et al. (2009)	COI, 28S, 18S, H3	FJ607574, FJ607538, FJ607500, FJ607612
Holarchaeidae	*Holarchaea* sp.	AToL ARACG000249	COI, 18S, H3	AToL unpublished sequence
Holarchaeidae	*Holarchaea* sp.	GenBank—Rix et al. (2008)	28S	EU302963
Pararchaeidae	*Ozarchaea platnicki*	AToL ARACG000286	COI, H3	AToL unpublished sequence
Pararchaeidae	*Nanarchaea binnaburra*	GenBank—Rix et al., 2008	28S, 18S	EU302964, EU302916
Desidae	*Badumna longinqua*	GenBank—Miller et al. (2010)	COI, 28S, 18S, H3	DQ628610, DQ628665, [DQ628738, DQ628701], DQ628637
Gnaphosidae	*Zelotes* sp.	GenBank—Spagna and Gillespie (2008)	COI, 28S, 18S	DQ628624, DQ628686, [DQ628759, DQ628722],
Gnaphosidae	*Zelotes* sp.	AToL ARAMR000525	H3	AToL unpublished sequence
Lycosidae	*Alopecosa kochi*	GenBank—Spagna and Gillespie (2008)	COI, 28S, 18S, H3	DQ628607, DQ628662, [DQ628735, DQ628698], DQ628635
Palpimanidae	*Palpimanus* sp.	Present study—9024279; extraction—0082	COI, 28S, 18S, H3	JX240235, [JX240274, JX240286], JX240255, JX240305
Huttoniidae	*Huttonia* sp.	Present study—9024279; extraction—Hutt41	COI, 28S, 18S, H3	JX240237, JX240288, JX240257, JX240307
Stenochillidae	*Colopea* sp.	Present study—9028424; extraction—0081	COI, 28S, 18S, H3	JX240236, JX240287, JX240256, JX240306
Mecysmaucheniidae	*Aotearoa magna*	Present study—9028246; extraction—0050	COI, 28S, 18S, H3	JX240238, [JX240275, JX240289], JX240258, JX240308
Mecysmaucheniidae	*Zearchea* sp.	Present study—9028243; extraction—0051	COI, 28S, 18S, H3	JX240242, [JX240279, JX240293], JX240262, JX240311
Mecysmaucheniidae	*Mesarchaea bellavista*	Present study—9027870; extraction—0040	28S, 18S	[JX240276, JX240290], JX240259
Mecysmaucheniidae	*Mesarchaea bellavista*	Present study—9019105; extraction—0020A	COI	JX240239
Mecysmaucheniidae	*Mecysmauchenius segmentatus*	Present study—9028435; extraction—0098	COI, 28S, 18S, H3	JX240240, [JX240277, JX240291], JX240260, JX240309
Mecysmaucheniidae	*Chilarchaea quellon*	Present study—9028089; extraction—0029	COI, 28S, 18S, H3	JX240241, [JX240278, JX240292], JX240261, JX240310
Archaeidae	*Eriauchenius lavatenda*	Present study—9018981; extraction—0003AB	COI, 28S, 18S, H3	JX240243, JX240294, JX240263, JX240312
Archaeidae	*Eriauchenius jeanneli*	Present study—9028293; extraction—0057	COI, 28S, 18S, H3	JX240244, JX240295, JX240264, JX240313
Archaeidae	*Eriauchenius legendrei*	Present study—9018992; extraction—0014	COI, 28S, 18S, H3	JX240245, JX240296, JX240265, JX240314
Archaeidae	*Eriauchenius workmani*	Present study—9018984; extraction—0006	COI, 28S, 18S, H3	JX240246, [JX240280, JX240297], JX240266, JX240315
Archaeidae	*Eriauchenius bourgini*	Present study—9028315; extraction—0061	COI, 18S, H3	JX240247, JX240267, JX240316
Archaeidae	*Afrarchaea* sp.	Present study—9018959; extraction—59Af3	COI, 28S, 18S, H3	JX240248, [JX240281, JX240298], JX240268, JX240317
Archaeidae	*Afrarchaea woodae*	Present study—9018957; extraction—57Af1	COI, 28S, 18S, H3	JX240249, [JX240282, JX240299], JX240269, JX240318
Archaeidae	*Austrarchaea nodosa*	Present study—9028388; extraction—0074	COI, 28S, 18S	JX240250, JX240300, JX240270,
Archaeidae	*Austrarchaea daviesae*	Present study—9023672; extraction—Au066	COI, 28S, 18S, H3	JX240251, [JX240283, JX240301], JX240271, JX240319
Archaeidae	*Austrarchaea mainae*	Present study—9028389; extraction—0075	COI, 28S, 18S	JX240252, JX240302, JX240272

For all taxa sequenced for the present study, the voucher number is from the California Academy of Sciences Entomology Department (CASENT), followed by the extraction number. For some taxa molecular data came from other sources, either from GenBank or from AToL (Assembling the Tree of Life Spider Project). Accession numbers in brackets show a sequence that is made up of two non-overlapping regions.

paradoxa and a female *Baltarchaea* sp.; although the taxon *Launauchenius speciosus* was scanned it was not used in this phylogenetic study (Appendix 6). From these scans, three-dimensional (3D) digital reconstructions were created which could be rotated and sliced through and examined to score characters (Fig. 1e). Characters were scored for the compression fossil *Patarchaea muralis* by examining the detailed published images (Selden et al., 2008).

Prey choice and predatory behaviour observations

To examine prey choice, prey specimens were collected with a spider specimen whenever a spider was observed in the field either stalking the prey or with prey captured in their chelicerae. The prey specimen was later identified to family. Additional observations were made on spider specimens that were reared in the laboratory and maintained on a diet of either laboratory-reared *Drosophila* or wild collected spiders. These observations include documentation of cheliceral movements during predatory attacks. In addition to the detailed examination of the carapace and chelicerae described above, the carapace and cheliceral morphologies were examined in juvenile specimens to determine how morphology changes with maturation, and was coupled with observations of the moulting process. Examination of juvenile morphology was done only on spider taxa with modifications to the carapace, such as presence of a diastema, foramen, or elevated cephalic area (''neck'').

DNA sequence collection and alignment

The majority of the molecular data used in this study were gathered using the methods listed below. Molecular data for some taxa, see Table 2, were also acquired from GenBank from the following studies: Wheeler and Hayashi (1998), Starrett and Waters (2007), Binford et al. (2008), Rix et al. (2008), Spagna and Gillespie (2008), Álvarez-Padilla et al. (2009), Arnedo et al. (2009), Blackledge et al. (2009), Duncan et al. (2010) and Miller et al. (2010). An additional eight unpublished sequences were acquired from the NSF Assembling the Tree of Life—Spiders project (AToL). Some of the sequences taken from GenBank and AToL were not as complete as the sequences generated in this study, and furthermore some specimens sequenced for this study were difficult to amplify and/or sequence for some markers, even though new primers were designed. For these two reasons, a few taxa are incomplete at some regions or markers, but the majority of the taxa are complete for all four markers (Table 2).

Prior to extraction, field-collected specimens were placed in 95% EtOH and stored in a freezer (−20 °C). A suite of primers was used to amplify a portion of the mitochondrial protein-coding gene Cytochrome *c* Oxidase subunit 1 (COI), the nuclear protein-coding gene Histone-3, and the ribosomal nuclear genes 28S and 18S. The four fragments were extracted, amplified and sequenced using standard protocols (Wood et al., 2007). Amplified PCR product was sequenced in the Evolutionary Genetics Lab at the Museum of Vertebrate Zoology at the University of California, Berkeley. Also, cleaned PCR product was sent to the UC Berkeley DNA Sequencing Facility for sequencing. All DNA sequences have been deposited in GenBank under accession numbers JX240233–JX240319 (Table 2).

The quality of forward and reverse sequences was confirmed using Sequencher version 4.7 (Gene Codes Co., Ann Arbor, MI, USA) by assembling forward and reverse sequences into aligned contigs. Consensus sequences were exported from each high-quality contig. Non-protein coding genes were aligned using the online interface (http://align.genome.jp/mafft/) for Mafft (Katoh et al., 2002) using the E-INS-i strategy, which operates best on sequences with multiple conserved domains and long gaps. The gap open penalty was set to the default of 1.5 and the offset value at the default of 0.14. Alignments were visually inspected using MacClade v4.08 (Maddison and Maddison, 2005) and no egregious errors were found. Protein coding genes were manually aligned, translated into amino acids and checked for stop codons using MacClade. The four gene alignments were then combined with the morphological data to form a concatenated data set using Mesquite v2.74 (Maddison and Maddison, 2010).

Phylogenetic analysis

Phylogenetic analyses were carried out using parsimony and Bayesian methods on each of the four individual genetic markers, the morphological data set, the four concatenated genetic markers and the concatenated molecular and morphological total-evidence (TE) data set. To examine how conserved regions of DNA (i.e. those regions without insertions or deletions) were contributing to the results, additional parsimony and Bayesian analyses were run with gapped regions manually removed from the TE concatenated data set, the concatenated genetic markers and the single marker data sets for 28S and 18S. Furthermore, to examine how incomplete taxa affect the phylogenetic results the fossil taxa were removed and additional analyses were performed on the TE data set and on the data set that contained only morphological characters. All analyses were rooted with the most basal Araneomorphae family Hypochilidae (*Hypochilus pococki* Forster, Platnick and Gray, 1987).

Parsimony searches were performed in PAUP* version 4.0b10 (Swofford, 2003) using the random stepwise addition option of the heuristic search for 1000 repli-

cates with tree bisection-reconnection (TBR) branch swapping, collapse of zero-length branches and equal weighting of all characters. All characters were treated as unordered and gaps were coded as missing data. To measure the robustness of branching patterns of the parsimony trees, bootstrap analyses (Felsenstein, 1985; Hillis and Bull, 1993) were executed for molecular data by using the random stepwise addition of the heuristic search for 1000 replicates. Bremer support values were also assessed using TreeRot v3 (Sorenson and Franzosa, 2007) for the morphology data set.

Bayesian analyses were implemented in MrBayes version 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Using the Akaike information criterion (AIC; Akaike, 1973), the best-fit substitution model was estimated for the genetic data using MrModeltest version 2.2 (Nylander, 2004) for 28S, 18S, and each of the three codon positions in the protein coding H3 and COI genes. The final concatenated TE data set had a total of nine partitions made up of the three codon positions for the two protein coding genes (six partitions), the two ribosomal nuclear markers and the morphological data. For the morphological partition, the standard discrete Markov model (Mkv) was used following Lewis (2001) with rates set to equal. Bayesian analyses were performed using four chains, the analysis was run twice simultaneously and the starting trees were randomly generated, with gaps coded as missing data. All analyses were run for 10 million generations, with sampling every 1000th generation, except for the four-gene-marker analysis with gapped regions removed and the analysis of only 28S with gapped regions removed (both run for 20 million generations) and the four-gene-marker analysis (run for 40 million generations), as these analyses took longer to converge. Additional Bayesian analyses of the TE data set were also performed to further explore the data. To examine how the priors were biasing the results (Brown et al., 2010; Marshall, 2010) analyses were performed with the branch length prior changed from the default value to more extreme values (short branch length: brlenspr = Unconstrained:Exp(100); long branch length: brlenspr = Unconstrained:Exp(1)). We also performed an analysis of the TE data where all partitions that were GTR + I + G were instead set to only GTR + G. This was done because it has been shown that I + G do not properly mix in analyses (Yang, 2006).

All Bayesian analyses were checked to ensure that the deviation of split frequencies was below 0.01. The two simultaneous analyses were evaluated for convergence using Tracer version 1.4 (Rambaut and Drummond, 2007). The burn-in value was visualized and determined by summarizing posterior distributions of scalar values, which identified the first 25% of the initial trees to be discarded, resulting in a final consensus tree with node support expressed as posterior probabilities. Morphological character reconstructions were performed on the TE Bayesian phylogeny in Mesquite v2.74 (Maddison and Maddison, 2010), using both parsimony and likelihood methods. Likelihood character reconstructions could not be performed on characters where taxa were scored as polymorphic. For visualization purposes, morphological characters were reconstructed on the tree using parsimony methods in WinClada version 2.0 (Nixon, 1999), optimized using the ''Slow'' command.

Results

Phylogenetic results

Our alignment resulted in a concatenated data set with 5311 characters, consisting of 658 bp for COI, 328 bp for H3, 2454 bp for 18S, 1745 bp for 28S and 126 morphological characters. Of the final concatenated data set, 2844 were variable sites, and 1910 of these were phylogenetically informative. In archaeid taxa the 18S and 28S markers had several areas with large insertions, the largest being 213 bp. The concatenated data set with non-conserved gapped regions removed (i.e. those regions with insertions or deletions) had 4205 bp, of which 2110 were variable sites, and 1578 of these were phylogenetically informative. In the analyses with removal of non-conserved regions of DNA, there were no topological conflicts and similar branch support values were recovered when compared with the analyses where all regions were retained. In the TE parsimony analysis, removal of non-conserved regions increased the resolution of the phylogeny, resulting in the recovery of a monophyletic Palpimanoidea (bootstrap = 59) and a monophyletic Entelegynae (bootstrap = 71). We conclude that, in this study, the conserved regions are the most important for reconstructing phylogenetic relationships. Additionally, removal of the fossil taxa did not alter the phylogenetic relationships among extant taxa. Regarding the additional Bayesian analyses performed on the TE data set, when the branch length prior was changed, the resulting topology and the relative rates of the partitions did not substantially change, and when the branch length prior was set to the default value the lowest and best likelihood score was recovered. These findings suggest that the branch length prior is not biasing the results. Also, the results did not change in the analysis where all partitions set to GTR + I + G were changed to GTR + G, suggesting that the analysis is not have mixing problems between I + G. In all analyses (with the exception of the analysis of only the morphological data) archaeid taxa and *Colopea* sp. have relatively long branch lengths, possibly due to an increased rate of molecular evolution.

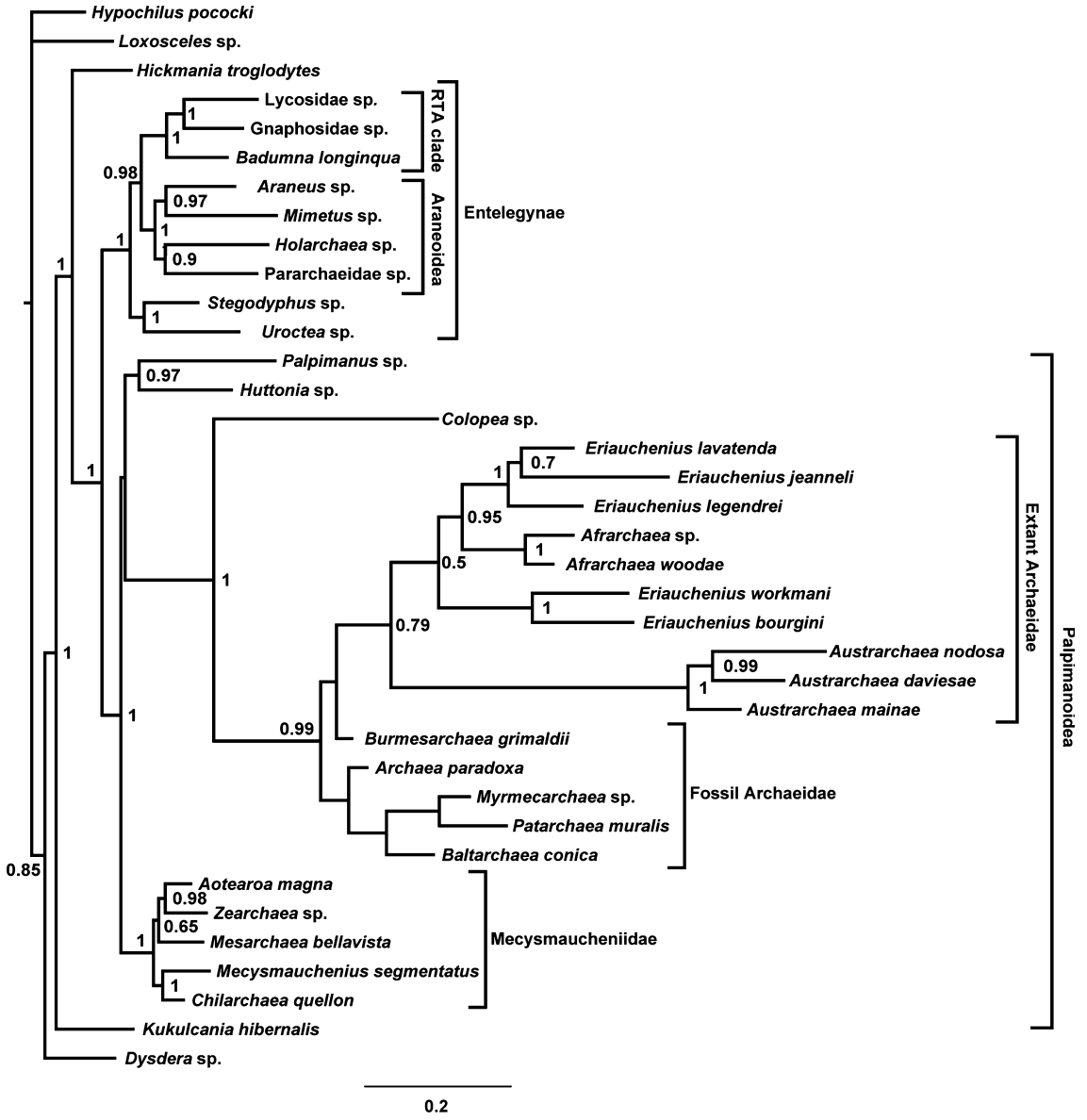

Fig. 2. Total-evidence phylogeny from Bayesian analysis of combined molecular and morphological data. Numbers at nodes represent posterior probabilities.

There were only minor differences between the parsimony and Bayesian analyses, with the parsimony analyses often having less topological resolution. Because of this we discuss only the results from the Bayesian analyses. The Bayesian results from the TE analysis, the concatenated four-molecular-marker analysis, and the morphological analysis are presented in Figs 2–4. The phylogenies that were recovered from the analysis of the individual morphological and molecular markers were sometimes topologically incongruent with the TE analysis and are presented in the Supplementary Information (Figs S1–S4). The parsimony results from the TE analysis, the concatenated four-molecular-marker analysis, and the morphological analysis are presented in Figs S5–S7. Parsimony and likelihood morphological character reconstructions were in agreement for the majority of characters. Differences in the parsimony and likelihood character reconstructions are noted in the Discussion and in Appendices 3–5, which focus on synapomorphies of the Palpimanoidea, Archaeidae and extant archaeids. For visualization purposes, morphological character optimizations using parsimony methods are shown in Figs S8 and S9.

Analyses of only the morphological data. The analyses of only the morphological data recovered a monophyletic Archaeidae and a clade containing only the extant

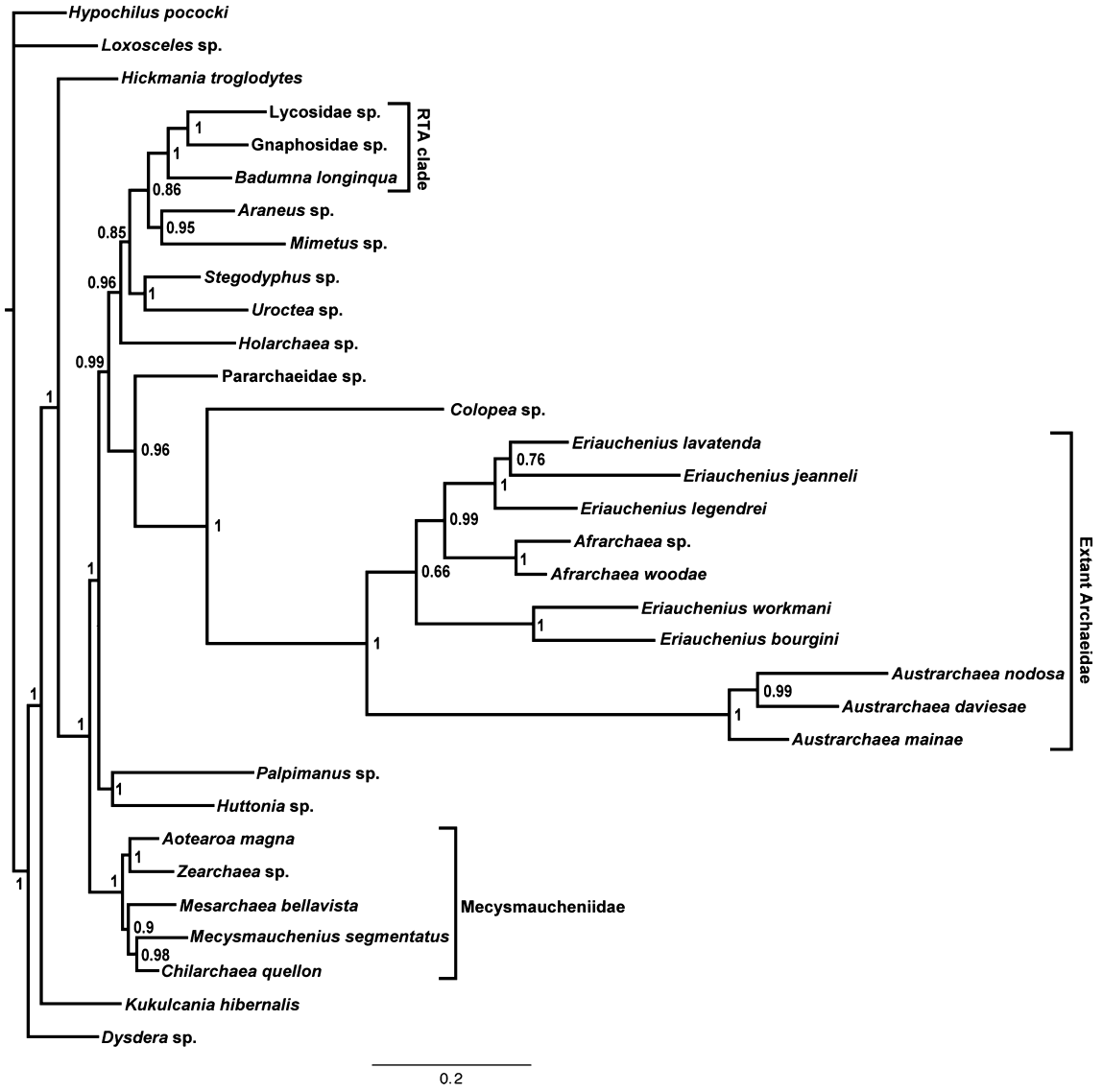

Fig. 3. Phylogeny from Bayesian analysis of concatenated molecular data. Numbers at nodes represent posterior probabilities.

archaeids (Fig. 4). The analyses also recovered a monophyletic Palpimanoidea that is nested within the Entelygynae clade.

Analyses of only the molecular data set. The analyses of the four-molecular-marker concatenated data set recovered a monophyletic Archaeidae (fossils are not included in the molecular data; Fig. 3). The molecular data recovered a paraphyletic Palpimanoidea.

TE analyses. We used the combined TE analysis as the best estimate of the phylogenetic relationships because this analysis incorporates multiple lines of evidence (Fig. 2). The Bayesian TE analysis recovered a monophyletic Archaeidae, and a monophyletic grouping of the extant archaeids, with the fossil archaeids falling outside. This analysis also recovered a monophyletic Palpimanoidea, to which the archaeids belong, which is sister to the monophyletic Entelegynae (''complex'' genitalia). Note that this resolution (Entelegynae as sister to the Palpimanoidea) arises from the interaction of morphology and molecules rather than from one source overcoming the signal from the other, as the morphology analysis found the Palpimanoidea to be derived entelegynes and the molecular analysis found the Entelegynae to be derived palpimanoids. In this analysis, the remaining taxa (*Hickmania troglodytes*, *Kukulcania* sp., *Dysdera* sp., *Loxosceles* sp., *Hypochilus pococki*), which are the more basal Araneomorphae, fall outside the Palpimanoidea + Entelegynae clade.

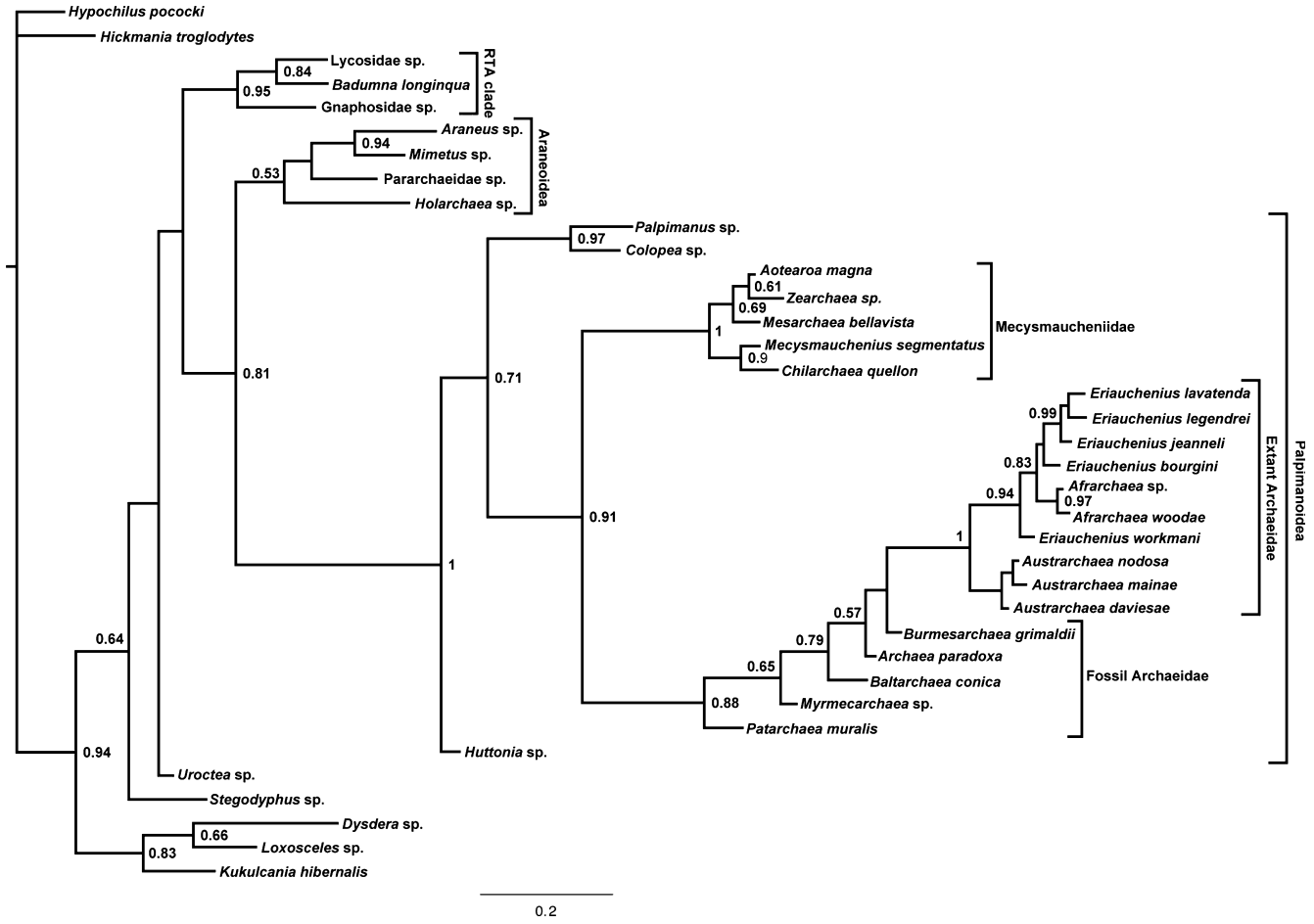

Fig. 4. Phylogeny from Bayesian analysis of morphological data. Numbers at nodes represent posterior probabilities.

Prey choice and predatory behavior observations

Prey choice field observations were only successful with the Madagascan archaeids since these taxa are abundant in the forests at night and easily observable, although one observation was recorded of a Chilean mecysmaucheniid species captured with another spider in its chelicerae. These results are reported in Table 3. Archaeids were observed stalking, capturing and feeding on Entelegynae spiders, although there were two observations of an archaeid with a dipteran in its chelicerae. Stalking is defined here as when the archaeid is in close proximity to the prey by being either on the spider prey's dragline, or at the edge of or invading the prey's web. Furthermore, while stalking, the archaeid is either plucking on the prey's web, is slowly approaching the prey, or is waiting in an attack posture with the front legs held up.

Laboratory observations were limited to specimens that could be reared successfully and included one huttonid (*Huttonia*), two stenochilids (*Colopea*), four palpimanids (*Palpimanus*), ten+ pararchaeids (all genus *Pararchaea* except for one *Anarchaea*), 100+ mecysmaucheniids (including representatives of all known extant genera except *Mesarchaea*) and 100+ archaeids (including all known extant genera). In the laboratory, archaeids, huttoniids, stenochilids and palpimanids would not eat laboratory-reared flightless *Drosophila*, even if they had not eaten for several weeks. Instead they were maintained on a diet of a variety of wild captured spiders. Pararchaeids rejected all food types and observations of cheliceral movements were only possible by agitating the specimen with an entomology pin with an eyelash glued to the tip. The majority of mecysmaucheniids could be maintained on a diet of laboratory-reared flightless *Drosophila*, but they would also eat spiders as well. A few mecysmaucheniid species would reject all food items, including *Drosophila* and spiders, and would only eat Collembola.

Cheliceral movements in huttoniids, stenochilids and palpimanids did not appear to deviate from typical spider cheliceral movements. In archaeids, upon close proximity to their prey, they swing both long chelicerae out and stab prey with both fangs at the tip, then they

Table 3
List of specimens observed stalking prey or with prey in their chelicerae

Specimens	CASENT	Locality	Prey	Collection time, event
Eriauchenius griswoldi (F)	9028284	MA, Kirindy	Thomisidae (juv.)	AM, prey in chelicerae
Eriauchenius griswoldi (F)	9028283	MA, Kirindy	Miturgidae (juv.)	PM, prey in chelicerae
Eriauchenius griswoldi (F)	9028282	MA, Kirindy	Uloboridae (juv.)	PM, prey in chelicerae
Eriauchenius griswoldi (F)	9028288	MA, Kirindy	Thomisidae (juv.)	PM, prey in chelicerae
Eriauchenius griswoldi (juv.)	9028285	MA, Kirindy	Pisauridae (F)	PM, stalking, walking into prey's web*
Eriauchenius griswoldi (F)	9028287	MA, Kirindy	Tetragnathidae (juv.)	PM, stalking, walking into prey's web
Eriauchenius jeanneli (F)	9028347	MA, Analamazaotra	Theridiidae (juv.)	PM, prey in chelicerae
Eriauchenius lavatenda (juv.)	9034222	MA, Ankarafantsika	Araneidae (juv.)	PM, prey in chelicerae
Eriauchenius tsingyensis (juv.)	9028342	MA, Ankarafantsika	Theridiidae (juv.)	PM, prey in chelicerae
Eriauchenius vadoni (juv.)	9028346	MA, Analamazaotra	Thomisidae (juv.)	PM, prey in chelicerae
Eriauchenius vadoni (juv.)	9028345	MA, Analamazaotra	Theridiidae (juv.)	PM, stalking, on prey's dragline
Eriauchenius vadoni (F)	9028351	MA, Analamazaotra	Cecidomyiidae (adult)†	PM, prey in chelicerae
Eriauchenius vadoni (F)	9028352	MA, Analamazaotra	Mycetophilidae (adult)†	PM, prey in chelicerae
Eriauchenius vadoni (juv.)	9028350	MA, Analamazaotra	Mysmenidae (M)	PM, prey in chelicerae
Eriauchenius vadoni (juv.)	9028349	MA, Analamazaotra	Mysmenidae (M)	PM, prey in chelicerae
Eriauchenius workmani (F)	9028367	MA, Ranomafana	Tetragnathidae (juv.)	PM, prey in chelicerae, at edge of prey's web
Eriauchenius workmani (juv.)	9028368	MA, Analamazaotra	Thomisidae (juv.)	PM, stalking, plucking on silk outside retreat
Eriauchenius workmani (juv.)	9028348	MA, Analamazaotra	Araneidae (juv.)	PM, prey in chelicerae
Mecysmauchenius sp. (F)‡	9034508	CH, Nahuelbuta	Anyphaenidae? (juv.)	PM, prey in chelicerae

CASENT, voucher number from the California Academy of Sciences Entomology Dept; MA, Madagascar; CH, Chile; AM, day collecting; PM, night collecting.

*The prey item was probably too large to be captured.

†Prey is identified to the family level; all prey are spiders, with the exception of two Diptera.

‡All specimens are archaeids, except for one mecysmaucheniid.

remove and lower only one chelicera and leave the other chelicera extended, holding the struggling prey impaled on the fang at the tip of the chelicerae far away (fig. 1 in Wood et al., 2007). Once the prey dies the chelicera is lowered to the mouthparts. Both pararchaeids and mecysmaucheniids are also capable of holding the chelicerae extended from the body at 90° (Fig. 5c,e). Their chelicerae movements were different from those of archaeids: prior to a strike their jaws would be held opened, seemingly locked in place, and long setae (''trigger hairs'') that are found on the inner margin of the chelicerae would be directed anterior (Fig. 5c,e). Stimulation of these setae caused the chelicerae to close. Examination of the cheliceral bases in mecysmaucheniids and pararchaeids suggests that the sclerite between the chelicerae bases interacts with the chelicerae bases, allowing them to be locked open.

The moulting process was only observed in archaeids. In juvenile archaeids there is a membranous anterior portion that runs lengthwise from the cheliceral bases to the mouthparts. The first stage of moulting involves the archaeid shedding the old carapace by squeezing through this membranous anterior portion. After this the specimen then sheds the cuticle on the abdomen, the ventral portion of the body and the legs, and the chelicerae.

Examination of juvenile carapace morphology was only performed on the Palpimanoidea, as defined in this study. In archaeids and mecysmaucheniids the membranous anterior opening or ''neck'' seam of the carapace, through which the specimen moults, becomes successively smaller as the spider progresses through its moults (see ''b'' in Fig. 5f). It is only in the adult specimens that the carapace edges are completely fused together (compare ''b'' in Fig. 5a,b with Fig. 5f). In juvenile palpaminids there are intercoxal sclerites that occur between the chelicerae bases and endites (mouthparts). These sclerites are not fused together in juvenile specimens, but in adult specimens they are fully fused together and to the carapace, which together form a foramen completely surrounding the cheliceral bases (Fig. 5d). Stenochilids are similar to palpimanids with the exception that in adults the midpoint seam of the intercoxal sclerites is not fused together, leaving a tiny gap. In huttoniids, which have a diastema (or space) between the cheliceral bases and endites, there were no differences in carapace morphology between juvenile and adult specimens.

Discussion

When possible, it is important to include fossils into the phylogenetic data matrix (Wiens, 2004), particularly useful for examining the evolution of a trait, such as has been done for evolution of avian flight (Gatesy and Dial, 1996). The fossil taxa in the current study were missing more than 95% of the data, yet they could still be phylogenetically placed using morphological characters.

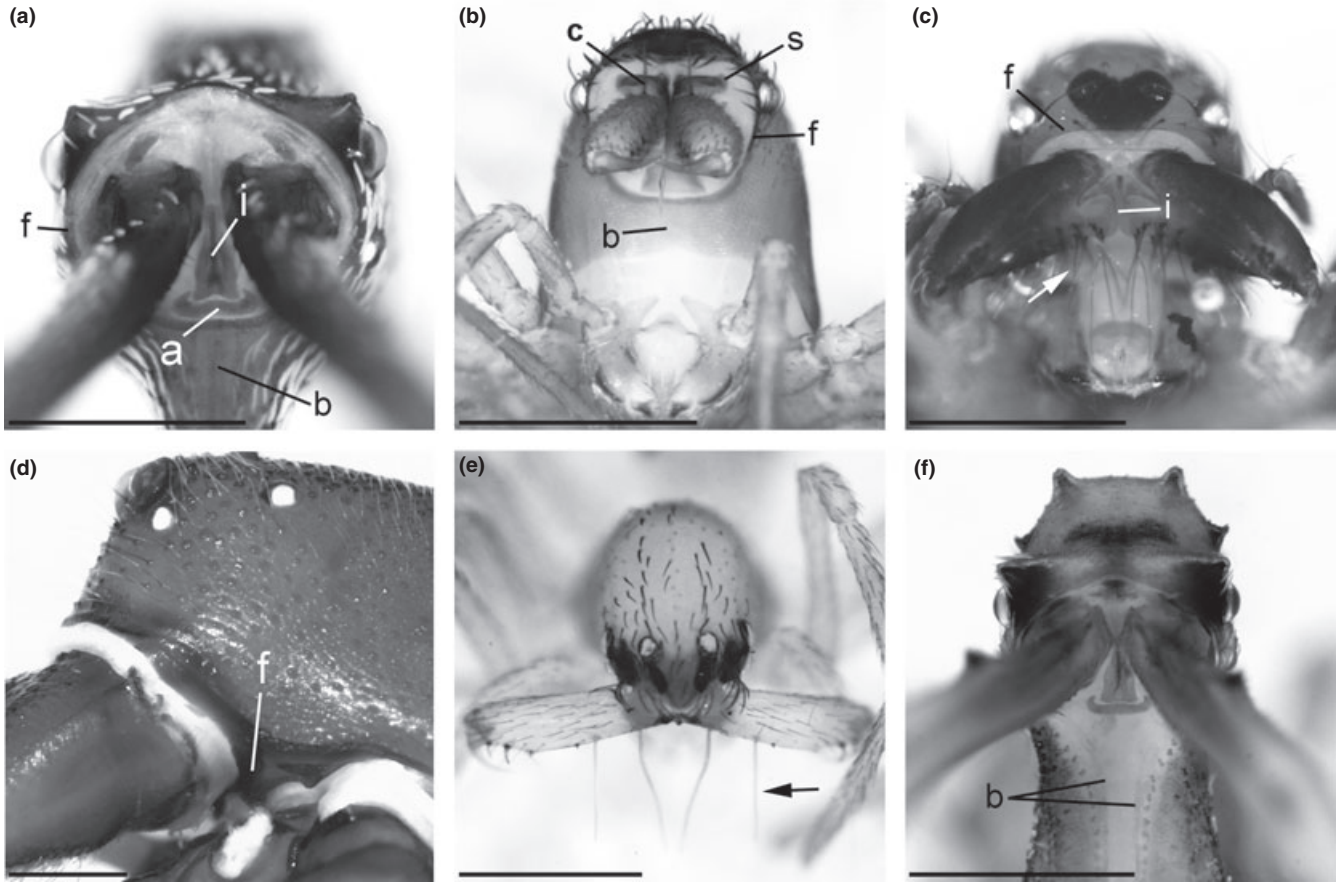

Fig. 5. Arrows show ''trigger hairs'', ''i'' shows the sclerite that rests between the cheliceral bases, ''f'' shows the foramen that surrounds the cheliceral bases, ''b'' shows the ''neck'' seam. (a) Archaeid, *Eriauchenius lavatenda* cheliceral bases, anterior–ventral, ''a'' shows an additional sclerite found beneath the inter-cheliceral sclerite. (b) Mecysmaucheniid, *Zearchaea* sp. cheliceral bases, anterior–ventral, with chelicerae closed, ''s'' shows the splayed cheliceral edge, ''c'' shows the spine on the anterior of the chelicerae. (c) Pararchaeid, *Anarchaea raveni* cheliceral bases, anterior–ventral. (d) Palpimanid, *Palpimanus* sp. cheliceral bases and carapace, lateral, palp removed. (e) Mecysmaucheniid, *Chilarchaea quellon* cephalothorax, dorsal, showing the highly manoeuvrable chelicerae. (f) Juvenile archaeid, *Eriauchenius vadoni* cheliceral bases, anterior–ventral, ''b'' shows membranous area of the ''neck'' in juveniles. Scale bars = 0.5 mm.

The TE Bayesian analysis recovers a phylogeny with a strongly supported topology (Fig. 2) and because the TE phylogeny was generated from multiple lines of evidence we consider this phylogeny to be the best current hypothesis of evolutionary relationships for these taxa. The phylogenies that were derived from the analysis of the individual morphological and molecular markers were sometimes topologically incongruent with the TE analyses (Figs S4–S8), possibly due to spiders being a very ancient group (Selden and Penney, 2010; Dimitrov et al., 2012), and their diversification may have been rapid and possibly confounded by the effect of homoplasy. In this study, even though the number of molecular characters greatly outnumbered morphological characters, the phylogenetic signal from the morphological data contributed to the results, which can be seen by comparing the topology from the phylogenies derived from the morphological, molecular and TE data sets.

Redefined Palpimanoidea

Subsequent to Forster and Platnick's (1984) expansion of Palpimanoidea, several studies have suggested that Palpimanoidea is paraphyletic; however, these studies did not fully address the placement of ousted members or the placement of archaeids. Using morphological characters, Schütt (2000, 2002) was the first to show that Palpimanoidea was not monophyletic, although this work did not adequately sample throughout the Araneomorphae in order to place archaeids. Other studies have also broken apart Forster and Platnick's Palpimanoidea, suggesting that the pararchaeids, micropholocomatines, holarchaeids and mimetids were misplaced in Palpimanoidea and group instead with orb-weavers and their relatives (Araneoidea; Rix et al., 2008; Blackledge et al., 2009; Dimitrov and Hormiga, 2011; Dimitrov et al., 2012), yet archaeids were not included in these studies, leaving their placement within the Araneomorphae unclear. A

phylogenetic study (Griswold et al., 2005), which relied on morphological data and included archaeids and other taxa from throughout the Araneomorphae, was ambiguous in its findings regarding archaeid placement: in the parsimony analysis with characters held under equal weights, archaeids and their Palpimanoidea relatives fell within the Entelygynae (''complex'' genitalia) and the monophyletic Palpimanoidea hypothesis was not refuted; whereas under the implied weights analysis, Palpimanoidea was split up and archaeids fell outside the Entelygynae.

In the present study, TE and morphology-only analyses support the monophyly of a redefined Palpimanoidea. According to these results, Palpimanoidea should be delimited to consist of the following families: Palpimanidae, Stenochilidae, Huttoniidae, Mecysmaucheniidae and Archaeidae. These results are in agreement with Forster and Platnick (1984) in the placement of Archaeidae and Mecysmaucheniidae within the ''traditional'' Palpimanoidea, but are not in agreement with the additional families included in their expanded Palpimanoidea. The current study does not address the placement of the Malkaridae, although Schütt (2000, 2002) and Dimitrov et al. (2012) found them to group within the Araneoidea. Our study is in agreement with the findings of Schütt that the expanded Palpimanoidea, as defined by Forster and Platnick (1984), should be broken up based on genitalic systems, such that families with ''complex'' (entelygyne) genitalia and those with ''simple'' (haplogyne) genitalia are not close relatives, but instead form two, distantly related clades. For a discussion of the morphological characters important for understanding evolution of the Palpimanoidea see Appendix 3.

Extant and fossil archaeid relationships

One aim of this study was to examine relationships among extant and fossil archaeids. There is strong morphological support for monophyly of the extant archaeids, which are restricted to the southern hemisphere: Madagascar, South Africa and Australia. Fossil archaeids, which are confined to the northern hemisphere, are paraphyletic with respect to the extant taxa, but relationships among fossil taxa are not well supported. There are several important morphological synapomorphies that are characteristic of the extant archaeids. For a complete discussion of the characters uniting the extant archaeids and the family Archaeidae, see Appendices 4 and 5. For a discussion of the enigmatic fossil *Lacunauchenius speciosus*, see Appendix 6.

Evolution of the modified carapace in the Araneomorphae

A leading idea in the historical classifications of archaeid spiders and their closest relatives has been that lineages with similarly modified and elevated cephalic areas (the ''neck'' and ''head'') are more closely related (Forster and Platnick, 1984). The only spider families that have a highly elevated pars cephalica (character 23) with a distinct ''neck'' and foramen are Archaeidae (Fig. 1e,g,h), Mecysmaucheniidae (Fig. 1f) and Pararcheidae (Fig. 1b). In this study, we find instead that lineages with elevated cephalic areas are not closely related and the likelihood and parsimony character reconstructions both suggest three independent origins: once each in archaeids and mecysmaucheniids, which belong to the Palpimanoidea but are not sister taxa, and once in pararchaeids, which belong to the Araneoidea. Recent research, which focused only on the Malagasy archaeid ''Gracilicollis group'', has shown that the length of the carapace may not be reliable for reconstructing phylogenetic relationships due to parallelism (Wood et al., 2007), and here we find that the evolution of the elevated cephalic area is also not reliable. Still, although lineages with extremely elevated cephalic areas are not closely related, it is important to note that they do appear to be closely related to ''intermediate'' lineages that have modifications to the cephalic area, discussed below, such as the remaining Palpimanoidea families or the family Holarchaeidae.

In typical spiders the carapace forms a convex plate that sits above the chelicerae and leg bases (see Fig. 1a), whereas in the spiders mentioned above that have an elevated cephalic area (or ''neck''), the carapace and chelicerae bases are lifted up, the chelicerae are elongated and the carapace forms a circle (a foramen) enclosing the base of the chelicerae: the plane of this circular opening is anterior (Fig. 5a–c). In spiders that have evolved a ''neck'', the muscles that attach the chelicerae bases to the carapace, which in other spiders run almost vertically (Palmgren, 1980), have changed orientation and run almost horizontally (Petrunkevitch, 1939; Legendre, 1965; our pers. observ.), running from the chelicerae bases to the back of the ''head'' rather than to the top of the carapace (compare bar in Fig. 1a with 1F). This unique orientation of the muscles, resulting from the evolution of the modified carapace, along with the anterior orientation of the carapace foramen, and the great extent of membranous cuticle around the chelicerae bases seems to have allowed archaeids, mecysmaucheniids and pararchaeids to have a much greater range of mobility in their chelicerae compared with typical spiders. This may allow for the chelicerae to be held horizontally, or 90° away from their body (Fig. 5c,e).

In this study we treat the trait of having a foramen surrounding the chelicerae bases (character 10) separately from the trait of having an elevated pars cephalica forming a ''neck'' (character 23). According to the likelihood and parsimony character reconstruction for character 10, the presence of a foramen is a synapo-

morphy for Palpimanoidea, which has evolved independently in pararchaeids and is lost in huttoniids. Yet, within Palpimanoidea, although there is a foramen surrounding the chelicerae bases, the elevated cephalic area or ''neck'' has only evolved in archaeids and mecysmaucheniids. Stenochilids and palpimanids have a foramen (arrow in Fig. 1c) that is derived from intercoxal sclerites (Fig. 5d), but the pars cephalica is not elevated. Archaeids and mecysmaucheniids have a foramen derived from the carapace (Fig. 5a,b) and there is a greatly extended pars cephalica or ''neck'' (Fig. 1e–h). In huttoniids, which have a carapace morphology similar to that shown in Fig. 1d, there is no foramen, nor is there an elevated pars cephalica, but there is a diastema (character 72) or space between the chelicerae and the endites (mouthparts). Regarding the evolution of these traits within the Araneomorphae, when the ''neck'' trait (character 23) is reconstructed onto the Bayesian TE analysis using both likelihood and parsimony methods, the elongated and elevated ''neck'' has evolved independently at least three times, once in the pararchaeids and twice in the Palpimanoidea (independently in the archaeids and mecysmaucheniids; Figs S8 and S9). This study demonstrates that archaeids, instead of being sister to mecysmaucheniids as previously thought based on the elevated carapace as well as a few other traits (Forster and Platnick, 1984), are sister to stenochilids, which do not have an elevated ''neck'' (Fig. 1d).

Regarding the character reconstructions for the ''neck'' and foramen (characters 10 and 23), it is important to note that the basal relationships within Palpimanoidea are not well supported. Because of this, character reconstructions may change in differently resolved phylogenies. For example, when the phylogeny is manually altered so that *Palipmanus* + *Huttonia* is the most basal group, rather than the mecysmaucheniids, likelihood character reconstructions reveal that the elevated ''neck'' (character 23) evolved only once within Palpimanoidea and was then lost in stenochilids, whereas parsimony reconstructions are ambiguous in whether the ''neck'' evolved twice or once and was lost. Regardless of the exact nature of these changes, whether the elevated carapace is independently evolving or is being lost, the important message is that there seems to be homoplasy within this trait.

Examining the chelicerae/carapace morphological modifications within the Palpimanoidea may be useful for understanding how the greatly extended pars cephalica (''neck'') evolved in both archaeids and mecysmaucheniids. In stenochilids and palpimanids the foramen encircling the chelicerae bases is formed by the carapace and intercoxal sclerites, which run between the endites (mouthparts; arrow in Figs 1c and 5d). This modification is not found in other spiders and could be the initial stage in the evolution of the extended ''neck''. The sclerotized bar, derived from the intercoxal sclerites, is fused with both sides of the carapace in adult specimens, but in juvenile specimens this bar is not completely fused and is made up of a few separate pieces. This suggests that the final sclerotized bar seen in adults is derived from sclerites that occur around the base of the legs and mouthparts (intercoxal sclerites) rather than as an outgrowth of the carapace. Huttoniids, on the other hand, do not have any modification between their chelicerae bases and mouthparts other than having a wide space (a diastema, character 72), which could also be an example of an intermediate initial state towards the evolution of the ''neck''. These two conditions offer two possible explanations for how, but not why, the evolution of the ''neck'' and the associated foramen surrounding the chelicerae bases occurred: (i) sclerites between the chelicerae and endites (mouthparts) began to get successively larger until they fused with the carapace, thereby completely encircling the chelicerae bases—this area later evolved into the greatly elevated and rigid ''neck'' and the seams that showed this fusion were lost; alternatively (ii) a wide space evolved between the chelicerae bases and the endites and the carapace began to successively wrap around to fill this area in until both edges of the carapace met and fused, forming a rigid circle around the chelicerae bases.

Developmentally, in archaeids and mecysmaucheniids the ''neck'' is derived from the carapace, which wraps further and further around the chelicerae bases as juvenile spiders progress through their molts (Fig. 5f; also see Legendre, 1962, for a description of the moulting process). It is not until the final moult into adulthood that the two edges of the carapace meet and fuse together, completely encircling the chelicerae bases (Fig. 5a,b). The development of the ''neck'' as juvenile mecysmaucheniids and archaeids progress through their moults argues for explanation (ii). Yet, it is intriguing that palpimanids and stenochilids have sclerotization that encircles the chelicerae bases, and that huttoniids have a diastema, suggesting the entire superfamily Palpimanoidea may have been predisposed to evolving a foramen encircling the chelicerae bases, which may have led to the evolution of the greatly elevated ''neck''.

Predatory behaviours in Palpimanoidea

While most spiders are generalist predators (Foelix, 2011), some members of the Palpimanoidea are known to be araneophages, meaning they are specialized to prey on other spiders. Araneophagy is also known to occur in other non-palpimanoid spiders such as mimetids (Jackson and Whitehouse, 1986), argyrodines (Agnarsson, 2004) and the salticid *Portia* (Li and Jackson, 1996; Clark and Jackson, 2000). Within Palpimanoidea, araneophagy has been mostly observed in the archaeids, for which it is obligatory for the most

part (Millot, 1948; Legendre, 1961; Wood, 2008) and in the palpimanids (Cerveira and Jackson, 2005; Pekar et al., 2011; our pers. observ.). Although we observed two instances of an archaeid preying on a fly (Table 3), it is likely that these Diptera were hanging from spider draglines at night when they were captured by the archaeid. It is unclear whether araneophagy evolved (or was lost) in the mecysmaucheniids, which appear to be generalists in captivity given that most species will eat both laboratory-reared flightless *Drosophila* as well as other spiders, although a few species will only eat Collembola. These findings are in agreement with the observations of Vellard (1957) that captive mecysmaucheniids ate flies, including *Drosophila*. Mecysmaucheniids are highly cryptic, making them difficult to observe in the field, but the one field observation we made involves a *Mecysmauchenius* sp. that was found with a partially eaten spider, probably an Anyphaenidae, in its chelicerae (Table 3). Vellard (1957) also observed a Chilean mecysmaucheniid that was captured in the field with a spider, also probably an Anyphaenidae, in its chelicerae. Furthermore, two additional field observations have been documented (M. Ramírez, pers. comm.): (i) a female *Mecysmauchenius fernandez*, observed on Juan Fernández Islands, was found inside a silken retreat that contained an eggcase that probably belonged to the Anyphaenidae spider *Sanogasta maculosa*, (ii) a female *Mecysmauchenius orsono*, observed in Parque Nacional Nahuel Huapi, Chile, was found on top of a silken retreat feeding on the Amphinectidae spider *Calacadia* sp. Although more data are needed, it is possible that some mecysmaucheniid species are specialized to feed on ground-dwelling hunting spiders, possibly by invading their retreats.

The predatory behaviours of huttoniids and stenochilids are unknown in nature, but they have similar modifications on their first pair of legs (thickened legs with spatulate hairs) as the araneophagic palpimanids. The first pair of legs, rather than the unusual chelicerae movements employed by the archaeids and mecysmaucheniids, are heavily utilized by palpimanids during predation in order to invade spider retreats and to touch the spider prey (Cerveira and Jackson, 2005; Pekar et al., 2011). Stenochilids and huttoniids, although based on a small number of specimen samples, were observed to readily eat spider prey in captivity and would not eat *Drosophila*. Archaeids (Table 3) and palpimanids (Cerveira and Jackson, 2005) seem to prey mostly on Entelgynae spiders. While other members of Palpimanoidea may be specialized for invading ground-dwelling spider retreats, archaeids seem specialized for invading spider webs. Given that the phylogenetic results of the current study showed Palpimanoidea to be sister to the Entelgynae, it is possible that Palpimanoidea diversification and evolution of their specialized predatory behaviours may have been parallel in time with Entelegynae diversification, and perhaps even a key to their survival. This highlights the need for more detailed knowledge of the predatory behaviours within the Palpimanoidea.

The evolution of the ''neck'' and ''head'', by changing the orientation of the chelicerae muscles so that they run almost horizontally rather than vertically (see bar in Fig. 1a,f), seems to have permitted spiders with this trait to evolve diverse and highly specialized chelicerae movements, possibly enabling access to previously unavailable predatory niches. The elevated pars cephalica, or ''neck'', in archaeids, mecysmaucheniids and pararchaeids appears to be an ecological trait, directly relating to the cheliceral movements used in predatory attacks and does not show sexual dimorphism. The araneophageous archaeids, with their manoeuvrable chelicerae, utilize an attack-at-a-distance predatory strategy by using their long chelicerae to hold their prey 90° away from their body, something that may have allowed them to successfully capture spider prey that has the potential to be injurious. The cheliceral movements of archaeids observed in this study are in agreement with previous observations (Legendre, 1961; Wood, 2008). The fossil archaeids have the same overall ''head'' and ''neck'' morphology as the extant species, although fossil taxa have shorter ''necks'' and chelicerae and the chelicerae are held at a slightly different orientation when at rest, being held so that the distal portion of the chelicerae point slightly anterior. As the fossil taxa have a ''neck'' and ''head'', which directly relates to the orientation of the cheliceral muscles, this suggests that fossil taxa were capable of a great degree of cheliceral mobility, similar to the extant taxa. This, and their phylogenetic placement, in turn suggests that ancient archaeids may also have been araneophageous.

The ''neck'' and chelicerae are robust and shorter in the distantly related pararchaeids and mecysmaucheniids, both of which have highly manoeuvrable chelicerae that are held open prior to a predatory attack, rather than being swung open and closed during the forward attack lunge. This behaviour was previously observed in pararchaeids (Rix, 2006). Vellard (1957) also noted that *Mecysmauchenius segmentatus* (Mecysmaucheniidae) would open its chelicerae and fangs widely and then swing them closed, thereby harpooning their prey with the fangs. The similar cheliceral movements utilized during an attack must have evolved independently as these two families are so distantly related.

There are other spider families with modifications causing elevations in the carapace. Holarchaeids appear to be intermediates: they have similar chelicerae/carapace organization as the archaeids, mecysmaucheniids and pararchaeids, and the pars cephalica is somewhat elevated and constricted, yet the ''neck'' and foramen is not completely formed. Holarchaeids were found in this study to be non-Palpimanoidea and closely related to

pararchaeids (Fig. 2), and it is unknown how they utilize their chelicerae during predation. In other spiders, such as the micropholcommatines, only the carapace is elevated, but the chelicerae bases are not raised as well (Forster and Platnick, 1984; Rix and Harvey, 2010). There are also examples of modifications to the carapace that are sexually dimorphic in nature, such as the raised eyes or raised processes on the carapace of male linyphiids (sheet-weaver spiders; Hormiga, 1999, 2000; Miller, 2007). Furthermore, there are spider families that have evolved greatly elongated chelicerae, yet have not evolved extreme modifications to the carapace, such as in the tetragnathid spiders (long-jawed orb-weavers; Álvarez-Padilla et al., 2009), although in the tetragnathid genus *Dolichognatha* not only are the chelicerae greatly elongated, but in some species the carapace is somewhat elevated as well (Smith, 2008). There is considerable variation in carapace shape among spiders and these modifications probably affect many aspects of a spider's lifestyle, such as sexual and predatory behaviour, ecology and prey choice. Here, we focused on only a small portion of that variation, looking at the specific modification of a foramen surrounding the chelicerae bases and the subsequent evolution of the ''neck''.

Conclusion

Based on these results, Palpimanoidea should be delimited to consist of the following families: Palpimanidae, Stenochilidae, Huttoniidae, Mecysmaucheniidae and Archaeidae. Several synapomorphies support this delimitation, including the presence of peg teeth and their occurrence on the retromargin of the chelicerae, that the male palp bulb expands distally, and the presence of sclerotization surrounding the cheliceral bases (does not occur in huttoniids), a modification on tarsus I, scopulae on the anterior legs (does not occur in mecysmaucheniids) and a cheliceral gland mound. Placement of fossil and extant archaeids within the Palpimanoidea has allowed for a better understanding of the evolutionary history of the lineage, and has provided a context for the evolution and diversification of ''neck'' morphologies in all spiders. All members of the redefined Palpimanoidea appear to have modifications to the carapace/chelicerae (e.g. diastema, foramen, elevated cephalic area), with only archaeids and mecysmaucheniids having evolved the extremely elevated ''necks''. The carapace/chelicerae modifications seen in the superfamily Palpimanoidea may have served as the groundplan, setting the stage for diversification along disparate paths, such as the evolution of the greatly elevated ''neck'' in archaeids. The cheliceral movements and predatory behaviours of spiders that have evolved elevated ''necks'' are atypical compared with most other spiders and may have allowed spiders with ''necks'' to occupy previously unavailable niches. Within the Palpimanoidea there appears to be a tendency toward araneophagy (predation on other spiders) with the evolution of highly specialized predatory behaviours. As Palpimanoidea is found to be sister to the Entelegynae and because their prey seems to be Entelegynae spiders, Palpimanoidea diversification may have been congruent with Entelegynae diversification, possibly specialized for predation on the Entelegynae.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Single marker phylogeny from Bayesian analysis of the molecular marker COI.

Fig. S2. Single marker phylogeny from Bayesian analysis of the molecular marker 18S.

Fig. S3. Single marker phylogeny from Bayesian analysis of the molecular marker 28S.

Fig. S4. Single marker phylogeny from Bayesian analysis of the molecular marker H3.

Fig. S5. Strict consensus from the combined total-evidence parsimony analysis, which recovered 160 trees of length 9454 [consistency index (CI) = 0.591, retention index (RI) = 0.528].

Fig. S6. Strict consensus from the parsimony analysis of concatenated molecular data, which recovered three trees of length 8897 (CI = 0.501, RI = 0.509).

Fig. S7. Strict consensus from the parsimony analysis of morphological data, which recovered 144 trees of length 342 (CI = 0.514, RI = 0.786).

Fig. S8. Morphological characters reconstructed onto the Bayesian total-evidence phylogeny, using slow optimization in WinClada.

Fig. S9. Morphological characters reconstructed onto the Bayesian total-evidence phylogeny for the Palpimanoidea taxa, using slow optimization in WinClada.

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Appendix 1

There are a total of 126 morphological characters used in the phylogenetic analysis. Inapplicable characters are coded (–) and data missing for characters are coded (?). Characters that are new or newly interpreted are discussed in detail; others are referenced to their original sources.

Somatic characters

1. Organized pairs of spines on carapace: absent, no carapace spines (0); two pairs (1); three pairs (2); four pairs (3); greater than four pairs, or in triplets (4). Mecysmaucheniids and archaeids have pairs of spines on their carapace that are very consistent in their placement and number. These also occur in *Mimetus* although these are more numerous and may be in triplets.

2. Spine next to lateral eyes: absent, no spines (0); one pair (1); two pairs (2). This character occurs in mecysmaucheniids, archaeids and *Mimetus*. See figure 18 of Wood (2008).

3. Anterior median eyes (AME): present (0); absent (1).

4. AME size: AME equal to or smaller than all other eyes (0); AME larger than all other eyes (1).

5. AME on tubercle: no (0); yes (1). The AME in archaeids are on a large tubercle.

6. Relative distance between median eyes: distance between AME less than distance between posterior median eyes (PME) (0); distance between PME less than distance between AME (1); AME-AME and PME-PME equal (2).

7. Tapetum: primitive (0); canoe shaped (1); grate shaped (2); absent (3) (Griswold et al., 2005 character 47).

8. PME shape: round (0); elongated (1).

9. Carapace texture: smooth (0); scales (1); tuberculate (2); fingerprint (3); pitted (4).

10. Foramen around cheliceral bases: absent (0); present (1). In pararchaeids, archaeids, mecysmaucheniids, *Palpimanus*, and *Colopea* the chelicerae bases are surrounded by sclerotized cuticle (Fig. 5a–d).

11. Foramen seam posterior to chelicerae: rebordered (0), as in Fig. 5a; smooth (1), as in Fig. 5b; seam not completely fused (2); thickened (3). This character is only applicable for taxa scored as present for character 10 and deals with the nature of the foramen seam.

12. Foramen formed around cheliceral bases: formed from intercoxal sclerites (0), as in Fig. 5d; formed from carapace (1), as in Fig. 5a–c. This character is only applicable for taxa scored as present for character 10 and records whether the foramen is formed from an extension of the carapace or from intercoxal sclerites.

13. Fovea: absent (0); present (1).

14. Posterior sternum tubercle: absent, posterior of sternum flat or evenly convex (0); mound (1); tubercle (2); two tubercles (3). In mecysmaucheniids and *Araneus* there is a mound at the posterior edge of the sternum. In extant archaeids there is a single tubercle (see fig. 9f in Wood, 2008) and in *Palpimanus* there are two.

15. Sternum border: absent (0); present (1). In several of the taxa in this study the edge of the sternum has a different texture and thickness from the rest of the sternum.

16. Chilum: absent (0); divided, bilateral (1); single, median (2) (Griswold et al., 2005 character 46).

17. Shape of sclerite between cheliceral bases: reduced rod (0); thick rod that interacts with cheliceral bases allowing chelicerae to be locked open (1); triangular (2), as in Fig. 5a; tear-drop shaped (3); fused to cheliceral bases allowing chelicerae to be locked open (4), as in Fig. 5c; two tear-drop shapes pointing toward each other (5). The shape of the sclerite between the chelicerae bases is variable among spider families. In pararcheids and mecysmaucheniids this sclerite interacts with the chelicerae bases allowing the chelicerae to be locked open (Fig. 5c,e), but the morphology is different in each family.

18. Additional rectangular sclerite beneath cheliceral base sclerite: absent (0); present (1), as in Fig. 5a. In archaeids there is an additional rectangular sclerite beneath the triangular cheliceral base sclerite of character 17, state 2.

19. Clypeal hood: absent, clypeal margin straight or concave (0); present (1) (Griswold et al., 2005, character 30).

20. Lateral labral spurs, two protrusions posterior to labral tongue: absent (0); present (1). Noted by Forster and Platnick (1984) as ''lateral protuberances found on the labrum''. This was scored as present in archaeids and mecysmaucheniids, but also in *Palpimanus* and *Colopea* where the lateral spurs are small and collapsed in SEM preparations (Fig. 6a,b). Our expanded interpretation differs from that of Platnick et al. (1991) character 49, where lateral labral protuberances were scored only for archaeids and mecysmaucheniids (Fig. 6c). Also, see fig. 93 of Miller et al. (2009) for images of the labral tongue and spurs.

21. Labium distal edge: straight to rounded (0); with narrow v-shaped notch (1); with shallow wide notch (2). Archaeids, *Mecysmaucheniu*s, *Palpimanus*, and *Dysdera* have a very narrow notch at the distal edge of the labium.

22. Posterior dorsal edge of pedicel with two elongations greatly extending into abdomen: absent (0); present (1), as in Fig. 7a. The posterior part of the pedicel (lorum 2) has two elongations that extend into the abdomen (Wilson, 1965). These elongations of the pedicel are pronounced in *Dysdera* and *Loxosceles*, and are extreme in *Palpimanus* (Fig. 7a) and *Colopea*.

23. Pars cephalica shape: unelevated (0); elevated (1) (Platnick et al., 1991; character 21; Griswold et al., 2005, character 31).

24. Raised cephalic area shape: tubular (0); constricted to form ''neck'' (1). Only applicable if character 23 is scored as present. This is present in archaeids and *Mesarchaea*: the most distal portion of the elevated cephalic area is wider than the stalk, creating a neck-like appearance (compare Fig. 1e,g,h with Fig. 1f).

25. Posterior edge of raised cephalic area shape is: flat (0); rounded out (1). Only applicable if character 24 is scored as present. This character refers to the posterior part of the cephalic area that is distal to the constriction, which is rounded out in *Mesarchaea* and some archaeids (Fig. 1h).

26. Endite length: less than half the carapace length (0); at least half the carapace length (1). Fossil archaeids have very long endites (Fig. 1e) whereas extant archaeids have shorter endites. Correlated with elongate endites are cheliceral stridulatory ridges being more basal than in extant archaeids. These features are correlated because in taxa with elongated endites the palps and chelicerae are at different orientations and the palps come in contact with the stridulatory ridges on the chelicerae.

27. Shape of posterior edge of carapace: gradually tapering off (0); flattened (1). In archaeids and *Palpimanus* the posterior edge of the carapace is truncated (Fig. 7b). This is best seen in the lateral view. In most spiders the carapace gradually tapers off.

Leg characters

28. Dorsal basal portion of tarsus 1: similar to rest of segment (0); with basal area of membranous or folded cuticle (1), as in Fig. 8a–f. Some modification of metatarsal cuticle appears to be present in all Palpimanoidea spiders. This interpretation differs from that of Platnick et al. (1991, character 50), which considered only the membranous ring encircling tarsus 1 as a synapomorphy for archaeids and mecysmaucheniids.

29. Type of modification on tarsus 1: large membranous bulge (0); membranous ring around tarsus (1); cuticular foldings (2). Modifications occur at the same place on the tarsus in Palpimanoidea and are coded as homologous. In *Colopea* and *Huttonia* there is a membranous tubercle that collapses when the leg is critically point dried (Fig. 8a,d). In *Palpimanus* there are foldings in the cuticle (Fig. 8b,e). In archaeids

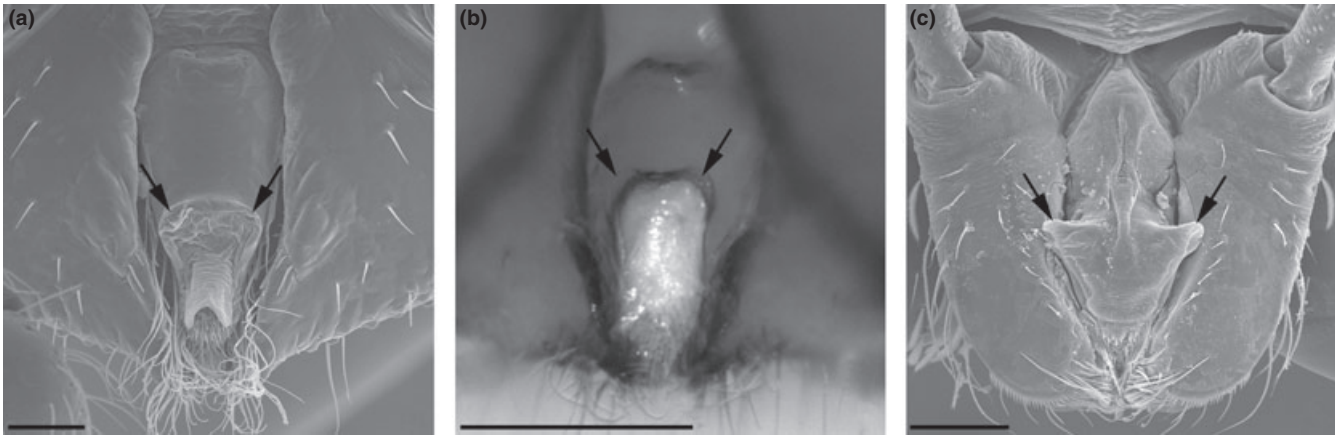

Fig. 6. (a) *Colopea* sp., SEM of labrum, dorsal, arrows showing reduced lateral spurs that collapse when critically point dried for SEM, image by J. Ledford. (b) *Colopea* sp. labrum, dorsal, arrows showing reduced lateral spurs. (c) *Eriauchenius lavatenda* labrum, dorsal, arrows showing lateral spurs. Scale bars: (a) and (b) = 100 μm, (c) = 0.25 mm.

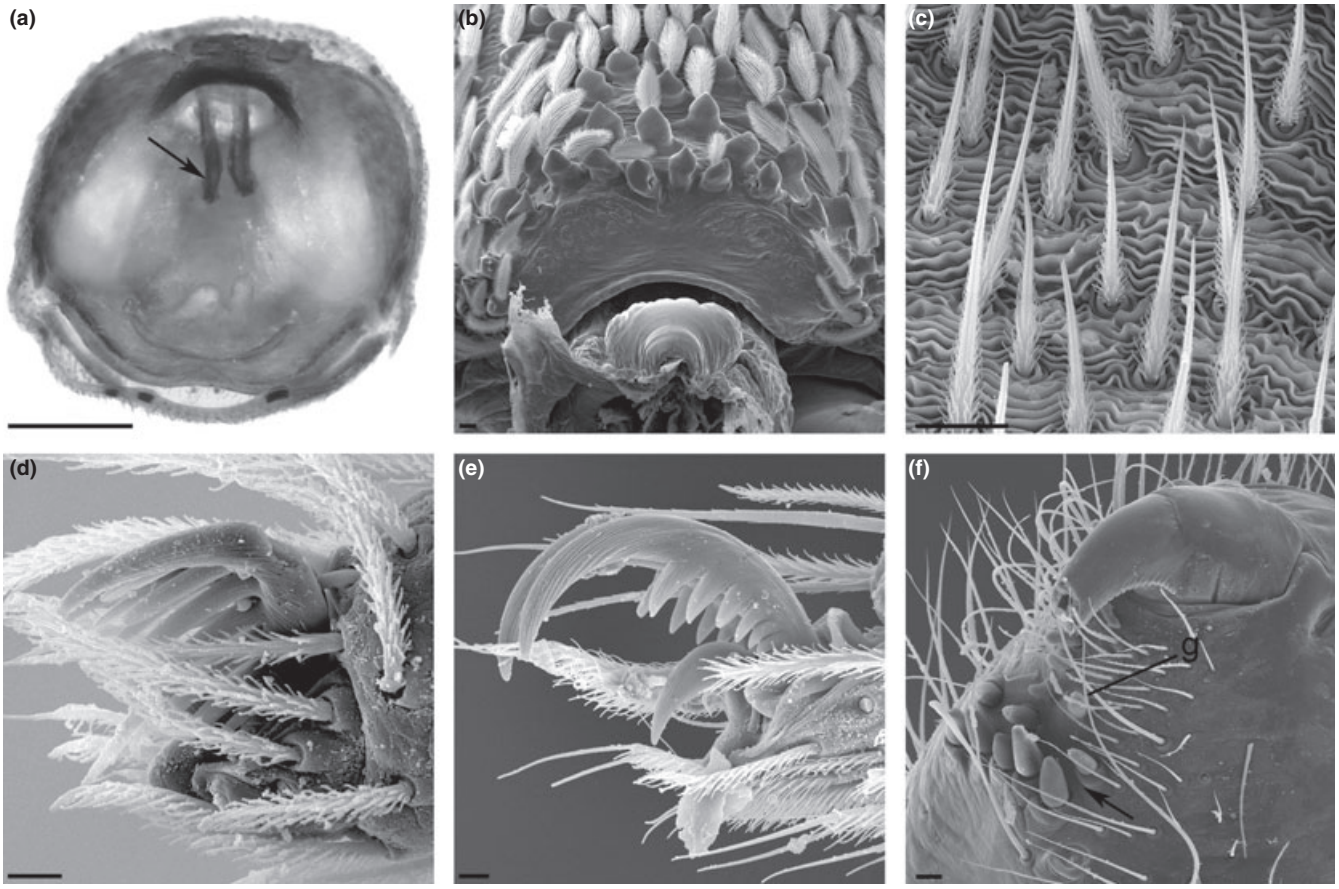

Fig. 7. (a) *Palpimanus* sp. cleared abdomen, dorsal–posterior, arrow showing elongated pedicel extensions. (b) *Eriauchenius lavatenda* carapace, posterior, showing truncated carapace. (c) *Colopea* sp. abdomen cuticle texture, image by J. Ledford. (d) *Mecysmauchenius* sp. claw I, retrolateral. (e) *Mecysmauchenius* sp. claw IV, retrolateral. (f) *Huttonia* sp. cheliceral retromargin, fang partially broken, arrow showing peg teeth on retromargin, "g" showing cheliceral gland mound. Scale bars: (a) = 0.5 mm, (b), (d) and (e) = 10 μm, (c) and (f) = 20 μm.

and mecysmaucheniids there is a membranous ring encircling the tarsus, previously noted by Forster and Platnick (1984; Fig. 8c,f).

30. Leg 3 metatarsus apical ventral setae: similar to other segment setae (0); distinct brush of setae different to setae on remainder of leg (1); comb of one row of setae (2); spines (3). Considered a preening comb (character 19) in Griswold et al. (2005), here we expand the definition to include a brush of setae as well as a comb. Only *Huttonia* has a comb (state 2), while *Kukulcania* and *Stegodyphus* have spines and archaeids, mecysmaucheniids, *Dysdera*, *Palpimanus*, and *Colopea* have a brush of setae.

31.Tarsal organ: exposed (0); capsulate (1) (Platnick et al., 1991; character 65; Griswold et al., 2005, character 2).

32. Shape of exposed tarsal organ: flat plate (0); with greatly elongated sensilla (1). Mecysmaucheniids have a uniquely shaped tarsal organ with long sensilla. See figures 104–115 and 178–179 of Forster and Platnick (1984).

33. Femur 4 shape: straight (0); with bend (1). The bent fumur 4 is present in most archaeid taxa with the exception of some fossil archaeids. See figure 7d of Wood (2008).

34. Dorsal surface of femora: smooth (0); with prominent bump (1). This bump is present in all archaeids.

35. Scopula on leg 1: absent (0); present (1).

36. Scopula leg 1 position: large prolateral group (0); prolateral row (1); one prolateral and one retrolateral row (2).

37. Scopula on leg 2: absent (0); present (1).

38. Patella and tibia juncture on leg 4: straight (0); bent, patella–tibia joint hyperextended (1). In archaeids the patella–tibia joint is hyperextended, most pronounced in leg 4.

39. Relative length of patella and tarsus 1: patella shorter than tarsus (0); patella longer than or equal to tarsus (1).

40. Relative shape and size of the superior tarsal claws (STC) 1 and 4: the same (0); STC 1 with many long teeth, like a comb (Fig. 7d), STC 4 with fewer teeth that are short and more widely spaced (Fig. 7e) (1); STC 1 smaller than STC 4 (2). In *Palpimanus*, *Huttonia*, *Colopea*, and mecysmaucheniids STC 1 are noticeably smaller than STC 4. In mecysmaucheniids and archaeids, STC 1 are shaped differently from STC 4 (Fig. 7d–e).

41. Tarsal claws: two (0); three (1) (Griswold et al., 2005, character 12).

42. Claw tufts: absent (0); present (1) (Griswold et al., 2005, character 13).

43. Trochanter distal margin: entire (0); deeply notched (1) (Griswold et al., 2005, character 11).

44. Tarsal trichobothria: absent (0); present (1) (Griswold et al., 2005, character 3).

45. Tarsal trichobothria rows: one row (0); two or more rows (1) (Griswold et al., 2005, character 4).

46. Metatarsal trichobothria: one (0); two (1); three or more (2) (Griswold et al., 2005, character 5).

47. Serrate accessory claw setae: absent (0); present (1) (Griswold et al., 2005, character 14).

48. Leg cuticle texture: fingerprint (0); squamate (1); smooth (2) (Griswold et al., 2005, character 10).

49. Leg hair type: plumose (0); serrate (1) (Griswold et al., 2005, character 17).

50. Trichobothrial base hood and texture: hood absent (0); smooth or same as leg texture (1); with transverse ridges (2) (Griswold et al., 2005, character 8).

51. Reduced leg spination: no (0); yes, with spines absent or limited to a few scattered examples (1) (Griswold et al., 2005, character 21).

Chelicerae characters

52. Chelicerae anterior surface: smooth (0); with spine or protuberance (1), as in Fig. 5b. *Mimetus*, mecysmaucheniids, and the extant archaeids have spines or protuberances on the anterior of the chelicerae.

53. Cheliceral modification in females: spine (0); bump (1).

54. Cheliceral modification in males: same as female (0); a brush of setae (1). In some taxa that have an anterior cheliceral modification, the males, unlike females, have a brush of setae. This is the case for *Austrarchaea* and *Chilarchaea*.

55. Basal edge of chelicerae: parallel (0); splayed out (1), as in Fig. 5b. In *Holarchaea*, mecysmaucheniids, and archaeids the basal edge of the chelicerae fans outward making the muscle attachment sites larger.

56. Cheliceral trigger hairs: absent (0); present (1). These are long modified setae with a modified base that are only found in Pararchaeidae and Mecysmaucheniidae (Fig. 5c,e). Stimulation of these setae causes the chelicerae to snap closed.

57. Trigger hairs distribution on chelicerae: scattered throughout the interior lateral side (0); in one evenly spaced row (1). In *Pararchaea*, unlike the mecysmaucheniids, the trigger hairs are scattered throughout the interior lateral side of the chelicerae (Fig. 5c).

58. Peg teeth: absent (0); present (1) (Platnick et al., 1991, character 19).

59. Peg teeth distribution on chelicerae: limited only to promargins (0); with some peg teeth on retromargin (1), as in Fig. 7f. In some of the taxa with peg teeth these may occur posterior to the area where the fang closes (the retromargin).

60. Two peg teeth in first row: absent (0); present (1). In archaeids and *Huttonia* there is an additional row of two peg teeth.

61. Thickened setae at fang base: absent, setae uniform (0); present, with a larger seta at fang base (1) (Griswold et al., 2005, character 34).

62. Stridulatory striae on chelicerae: absent, surface smooth (0); present (1) (Griswold et al., 2005, character 45).

63. Texture of stridulatory striae (in males): uniform and densly spaced fingerprint ridges (0); widely spaced uniform ridges (1); widely spaced heterogeneous ridges (2); rounded bumps (3); uneven small ridges (4).

64. Shape of chelicerae distad of stridulatory ridges: straight (0); curved toward posterior (1). The distal portion of the chelicerae are curved to posterior only in extant archaeids (Fig. 1g,h).

65. Peg teeth shape: straight, tapering, smooth (0); straight, blunt, textured (1); curved, tapering, textured.

66. Promarginal row of peg teeth: uniform lengths (0); with different lengths (1).

67. Cheliceral gland mound: absent (0); present (1). Like Griswold et al. (2005), character 42, we scored *Mimetus* as absent for this trait. We also differed from this and previous assessments in scoring our pararchaeid exemplar as absent for this trait. The voucher specimen for the morphological data was species *Ozarchaea platnicki* from Mount Bartle Frere in Australia: in this specimen there was a ridged spur adjacent to the keel (see figs 227 and 230 of Forster and Platnick, 1984), but there was no associated gland mound with pores.

68. Cuticle adjacent to cheliceral gland mound: flat (0); with deep groove (1). In archaeids there is a deep groove immediately adjacent to the gland mound.

69. Cheliceral boss: absent (0); present (1) (Griswold et al., 2005, character 43).

70. Cheliceral chela: absent (0); present (1) (Griswold et al., 2005, character 40).

71. Cheliceral basal fusion: free (0); fused (1) (Griswold et al., 2005, character 38).

72. Cheliceral diastema: absent (0); present (1). We scored this character as present for *Palpimanus* (Figs 1c and 5d) and *Colopea* because these taxa have a sclerotized piece or pieces between the endites and the chelicerae; see character 10.

Abdomen characters

73. Abdomen shape: smoothly curved (0); with tubercles (1). Several archaeid taxa have tubercles on the abdomen.

74. Abdomen tubercles placement: in pairs (0); singular (1).

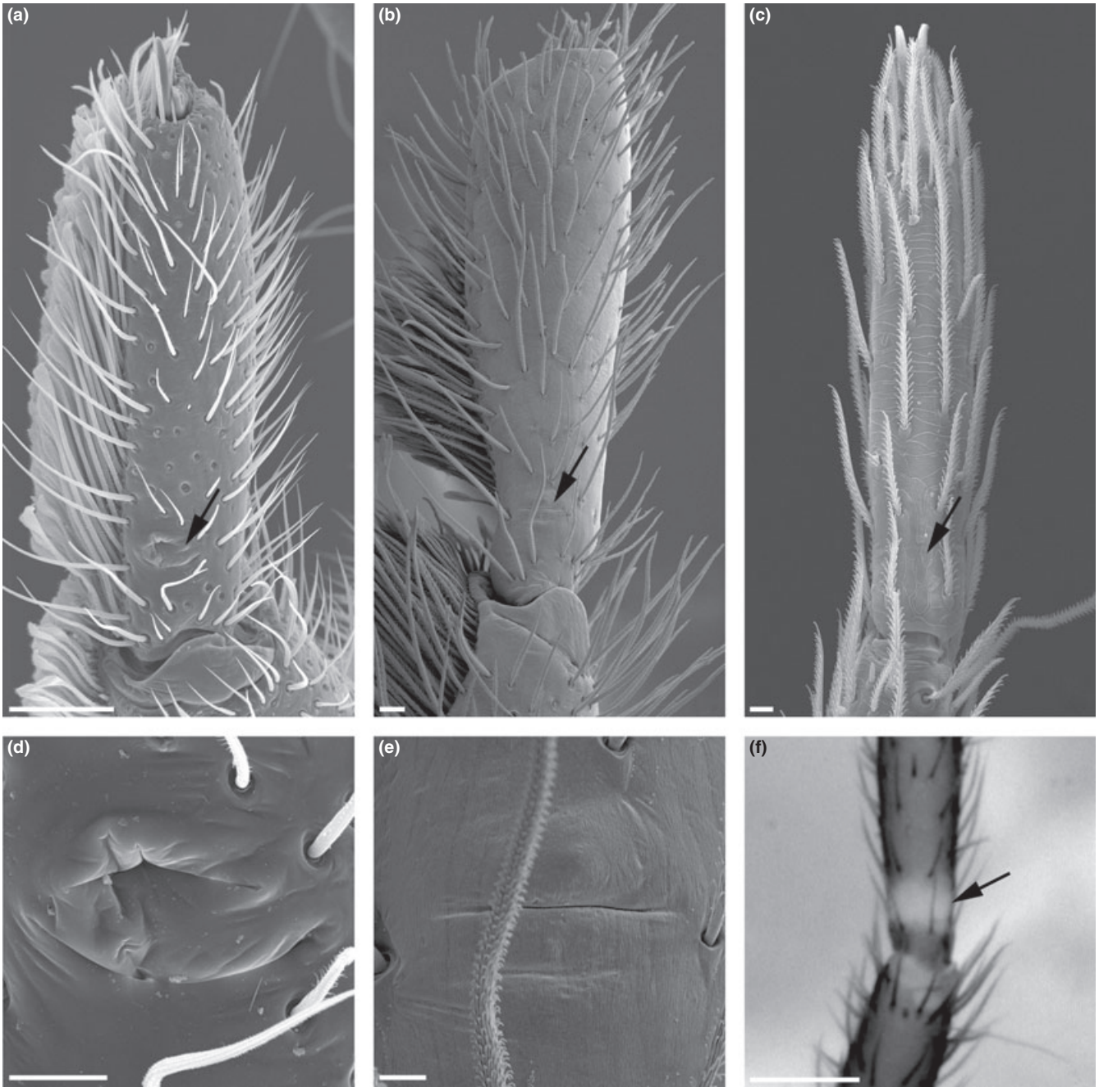

Fig. 8. (a, d) *Colopea* sp. tarsus I, dorsal, images by J. Ledford. (b, e) *Palpimanus* sp. tarsus I, dorsal. (c) *Chilarchaea quellon* tarsus II, dorsal. (f) *Mecysmauchenius* sp. distal portion of tarsus I, prolateral. Arrow showing tarsal modification, (d)–(f) close-up view. Scale bars: (a) = 100 μm, (b) = 30 μm, (c) and (e) = 10 μm, (d) = 20 μm, (f) = 0.1 mm.

75. Posterior respiratory system: pair of normal booklungs (0); pair of reduced booklungs (1); pair of tracheae or modifications thereof (2). Following Platnick et al. (1991), character 16, which does not differentiate between lateral and median tracheae, archaeids are scored as state 2. *Kukulcania* is scored as having reduced booklungs, state 1, following Griswold et al. (2005).

76. Posterior spiracle: single (0); double (1) (Griswold et al., 2005, character 60).

77. Dorsal abdominal scutum on male: absent (0); present (1). This is seen in some archaeids and our gnaphosid exemplar.

78. Epiandrous spigots: absent (0); present (1) (Griswold et al., 2005, character 66).

79. Posterior spinnerets: medians developed, laterals about as large as anterior laterals (0); very reduced (1). The posterior spinnerets are very reduced in *Palpimanus*, *Colopea* and the mecysmaucheniids, with

the spigots either arising directly from the abdominal cuticle or from highly reduced spinnerets.

80. Spigot base texture: fingerprint (0); smooth (1); scaly (2). Modified from Griswold et al. (2005), character 69.

81. Sclerotization around anterior of abdomen: absent (0); present (1).

82. Modification of sclerotization around anterior of abdomen in females: dorsal and ventral sclerites separate (1); dorsal and ventral sclerites fused (2); only ventral plate present, dorsal plate absent (3).

83. Abdomen with folds: absent (0); present (1). This character is present in all archaeids and is discussed by Forster and Platnick (1984). This trait is especially apparent in the fossil taxa (Fig. 1e), but is also apparent in living taxa, particularly specimens with shrunken abdomens.

84. Abdomen cuticle highly wrinkled when critically point dried (Fig. 7c): absent (0); present (1). This feature is imaged in Forster and Platnick (1984), fig. 41) but not discussed. In several taxa in this study the abdomen is peculiarly wrinkled when prepared for SEM imaging by critical point drying.

85. Spinnerets projected on conical tubercle: absent (0); present (1). The spinnerets arise from a conical tubercle in archaeids (Fig. 1e).

Female palp characters

86. Brush of hairs on female palpal tarsus (also on male cymbium): absent (0); present (1). We also score this as present if there is a brush on the male cymbium.

87. Placement of palpal brush on tarsus: on prolateral side (0); on retrolateral side (1).

88. Picks on palpal femur: absent (0); at least one cusp present (1). These picks probably come in contact with the stridulatory file on the chelicerae.

89. Prolateral spines on female palp tarsus: absent (0); present (1).

90. Placement of female palp spines: scattered (0); one row (1). In mecysmaucheniids the tarsal spines on the palp are in one row.

91. Female palp claw: absent (0); present (1); very reduced, for example only a nubbin (2). Modified from Platnick et al. (1991), character 37.

Female genitalic characters

92. Female genitalia: haplogyne (0); entelegyne (1).

93. Female sclerotized genital plate (FSGP): absent (0); present (1). See Wood (2008, p. 259) for description of this character.

94. FSGP with wings: absent (0); present (1). See Wood (2008, p. 259) for description of this character.

95. FSGP with keel: absent (0); present (1). The FSGP in *Afrarchaea* has a keel (see fig. 58 in Forster and Platnick, 1984).

96. Membranous sacs (receptaculae) originating from bursa: absent (0); present (1). *Hickmania* and all Palpimanoidea families are scored present for this character, although this character is absent in the African and Malagasy archaeids (see figs 66–69, 210, 211, 295–299 of Forster and Platnick, 1984).

97. Distribution of bursal membranous sacs: dispersed evenly all over bursa (0); clustered and originating from one or two openings on the bursa (1). In *Austrarchaea* and some mecysmaucheniids the genitalic membranous sacs are dispersed over the bursa. In the remaining Palpimanoidea these sacs are clustered. Although this character is not broken down further, it is important to note that only in the New Zealand mecysmaucheniids (*Aotearoa* and *Zearchaea*) does this cluster join to the centre of the bursa, whereas in other palpimanoids, e.g. *Huttonia*, *Colopea*, and *Palpimanus*, these clusters originate from the lateral sides of the bursa.

98. Membranous sac shape: large sacs sessile, not on stalks (0); sacs on long stalks (1). Compare figs 210 and 211 with figs 66–69 in Forster and Platnick (1984). Only in the *Austrarchaea* and *Colopea* are the genitalic membranous sacs sessile.

Male genitalic characters

99. Fusion of tegulum and subtegulum: absent, tegulum and subtegulum free (0); fused, bulb piriform (1) (Griswold et al., 2005, character 114).

100. Palp rotated with cymbium prolateral and bulb retrolateral: absent (0); present (1). See Griswold et al. (1998), character 2, for a discussion of this character.

101. Conductor: absent (0); present (1) (Griswold et al., 2005, character 118).

102. Conductor shape: conductor separate from embolus (0); conductor embraces embolus (1) (Griswold et al., 2005, character 120).

103. Median apophysis: absent (0); present (1) (Griswold et al., 2005, character 123).

104. Palpal tarsus M30 muscle: absent (0); present (1) (Griswold et al., 2005, character 129).

105. Palpal tarsus M29 muscle: absent (0); present (1) (Griswold et al., 2005, character 128).

106. Paracymbium: absent (0); present (1). The paracymbium in this study was treated as any type of apophysis on the retrolateral side of the cymbium (Griswold et al., 2005, character 112).

107. Shape of paracymbium: protrusion with thick spine or setae (0); cluster of long setae not on protrusion (1); long curved apophysis (2).

108. Retrolateral apophysis on femur: absent (0); present (1).

109. Retrolateral apophysis on patella: absent (0); present (1).

110. Retrolateral apophysis on tibia (RTA): absent (0); present (1) (Griswold et al., 2005, character 105).

111. Shape of RTA: protrusion at distal edge (0); protrusion with thick seta (1); many thick setae not on protrusion (2); complex, two to four processes (3).

112. Tegulum: entire, surface smooth (0); with sulcus (1). Mecysmaucheniid spiders have a characteristic sulcus that divides the tegulum. This trait was also observed in *Austrarchaea* by Forster and Platnick (1984). In this study *Austrarchaea* was coded as ''smooth'' for this character because the tegular shapes and the placement of the sulcus is different between mecysmaucheniids and archaeids. See fig. 207 of Forster and Platnick (1984).

113. Shape of bulb apex: apex of bulb without a dark ridged spiral (0); with a dark ridged spiral forming a conductor (1). Most archaeids have a dark ridged spiral at the apex of the bulb, which has been scored as the ''conductor'' (Griswold et al., 2005, fig. 168d).

114. Palpal bulb expands distally (Fig. 9a–c): no, there is only a basal expansion of the palpal bulb, although distal portions may still move and un-twist (0); yes (1). In all spiders in this study the palp bulb expands basally, close to the attachment to the cymbium. Yet, only in some taxa does the bulb also expand distally (Fig. 9a–c), with membranous tissue ballooning out at the apex of the bulb. In this study, this character is unique to the Palpimanoidea, although *Araneus* was also coded as present for this character as distal parts of the araneid bulb have moveable joints.

Spinneret characters

115. Cribellum: absent (0); present (1) (Griswold et al., 2005, character 71).

116. Cribellum organization: entire (0); divided (1) (Griswold et al., 2005, character 72).

117. Cribellate spigots: strobilate (0); claviform (1) (Griswold et al., 2005, character 74).

118. Posterior median spinnerets (PMS) paracribellar gland spigots in females: absent (0); present (1) (Griswold et al., 2005, character 88).

119. PMS paracribellar gland spigots in male: absent (0); present (1) (Griswold et al., 2005, character 89).

120. Posterior lateral spinnerets (PLS) paracribellar gland spigots in females: absent (0); present (1) (Griswold et al., 2005, character 99).

121. PLS modified spigot: absent (0); present (1) (Griswold et al., 2005, character 96).

122. ALS major ampullate gland spigot (MAP) field separated by furrow: absent (0); present (1). This character was difficult to score because it seems to be continuous (Griswold et al., 2005, character 77).

123. ALS segment number: three (0); two (1) (Griswold et al., 2005, character 75).

124. Tartipores: absent (0); present (1) (Platnick et al., 1991, character 63).

125. PMS minor ampullate gland spigot (mAP) postion: median to anterior (0); posterior (1); absent (2). (Griswold et al., 2005, character 83).

126. Cylindrical gland spigots: absent (0); present (1) (Platnick et al., 1991, character 23).

Appendix 3: Palpimanoidea synapomorphies

Rather than discussing all 126 characters in detail, we discuss only the morphological characters that are useful and important for understanding evolution of the Palpimanoidea; other characters are optimized on the TE Bayesian tree (Figs S8 and S9). Character reconstructions were performed using both parsimony and likelihood methods, and the results were similar (meaning the most favourable likelihood reconstruction was the same as the parsimony reconstruction) unless otherwise stated. It is important to note that the basal relationships within Palpimanoidea are not well supported so that character optimizations may change in the future. Although this trait is lost in huttoniids, all Palpimanoidea have a sclerotized foramen encircling the base of the chelicerae (character 10), which may take the form of a narrow rod that runs between the chelicerae and mouthparts (labrum, endites, and labium), as in palpimanids and stenochilids, or as a modification of the carapace, as in archaeids and mecysmaucheniids. This trait also evolved independently in Pararchaeidae. Another Palpimanoidea synapomorphy is the presence of a border on the sternum (character 15), which also independently evolved in *Dysdera* sp. The labrum, a mouthpart structure, has two spurs (character 20, Fig. 6), which are lost in huttoniids, and that are greatly reduced, as in stenochilids (Fig. 6a,b) and palpimanids, or very prominent, as in archaeids (Fig. 6c) and mecysmaucheniids. Within Palpimanoidea, all members have the synapomorphy of a modification on the dorsal, basal side of tarsus 1 (character 28, Fig. 8), which can be a membranous bulge (Fig. 8a,d) or ring (Fig. 8c,f), or cuticular foldings (Fig. 8B,E). There is a brush of hairs on metatarsus III (character 30), which is a comb in *Huttonia* sp. and which evolved independently in *Dysdera* sp. Although this synapomorphy is lost in archaeids, in Palpimanoidea claw I is smaller than claw IV (character 40, Fig. 7d,e). With the exception of being lost in *Chilarchaea*, all Palpimanoidea taxa share the trait of transverse ridges on the trichobothrium hood (character 50), and these ridges also occur independently in *Loxosceles*, *Stegodyphus*, and other entelegynes. There is also a reduction in leg spination (character 51), a trait that also appears independently in several other taxa in this study. Palpimanoidea have modified hairs on the chelicerae (character 58), termed "peg-teeth", which are lost in

Appendix 2: Morphological character matrix. Terminals scored with more than one state are coded as: a = (0 & 1); b = (1 & 2)

	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 5 5 5 5 6 6 6 6 6 6 6 6 6 6 7
Character	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
Hypochilus pococki	0 0 0 0 0 0 0 0 0 0 - - 1 0 0 0 0 0 0 0 0 0 0 - - 0 0 0 - 0 0 0 0 0 0 - - 0 0 0 1 0 0 0 - 0 0 0 0 1 1 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 0 0
Hickmania troglodytes	0 0 0 0 0 0 0 0 0 0 - - 1 0 0 0 0 0 1 0 2 0 0 - - 0 0 0 - 0 0 0 0 0 0 - - 0 0 0 1 0 0 0 - 0 1 0 0 1 0 0 - - 0 0 - 0 - - 1 1 3 0 - - 0 0 0 0
Lycosidae *sp*	0 0 0 0 0 0 2 0 3 0 - - 1 0 0 1 0 0 0 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 0 0 0 1 0 1 1 1 2 0 0 1 1 0 0 - - 0 0 - 0 - - 1 0 - 0 - - 0 0 1 0
Araneus sp	0 0 0 0 0 1 1 0 1 0 - - 1 1 0 1 0 0 0 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 0 1 0 1 0 1 0 - 0 1 1 1 0 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 1 0
Badumna longinqua	0 0 0 1 0 0 1 0 3 0 - - 1 0 0 1 0 0 0 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 0 1 0 1 0 0 1 0 2 0 0 0 1 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 1 0
Dysdera sp	0 0 1 - - - 0 0 0 0 - - 0 0 1 2 0 0 0 0 1 1 0 - - 0 0 0 - 1 0 0 0 0 0 - - 0 1 0 0 1 0 0 - 0 0 0 0 0 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 0 0
Holarchaea sp	0 0 0 0 0 0 ? 0 4 0 - - 0 0 0 0 - 0 1 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 1 0 0 1 0 0 0 - 0 1 1 a 1 0 0 - - 1 0 - 0 - - 0 0 - 0 - - 1 0 0 0
Kukulcania hibernalis	0 0 0 0 0 0 0 1 0 0 - - 1 0 0 0 0 0 0 0 0 0 0 - - 0 0 0 - 2 1 - 0 0 0 - - 0 0 0 1 0 0 0 - 2 0 2 0 0 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 0 1
Loxosceles sp	0 0 1 - - - 0 0 0 0 - - 1 0 0 0 0 0 0 0 0 1 0 - - 0 0 0 - 0 0 0 0 0 0 - - 0 0 0 0 0 0 0 - 0 0 2 a 2 1 0 - - 0 0 - 0 - - 0 1 4 0 - - 0 0 0 1
Mimetus sp	4 2 0 1 0 1 1 0 1 0 - - 1 0 0 0 0 0 0 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 0 0 0 1 0 0 0 - 0 1 1 1 0 0 1 0 0 0 0 - 1 0 0 0 0 - 0 0 0 0 0 0 0
Pararchaeidae *sp*	0 0 0 0 0 0 1 0 1 1 2 1 0 0 0 0 4 0 0 0 0 0 1 0 - 0 0 0 - 0 1 - 0 0 0 - - 0 0 0 1 0 0 0 - 0 1 1 1 1 1 0 - - 0 1 0 1 0 0 0 0 - 0 1 0 0 0 0 0
Stegodyphus sp	0 0 0 0 0 0 3 0 0 0 - - 0 0 0 0 3 0 1 0 0 0 0 - - 0 0 0 - 2 1 - 0 0 0 - - 0 1 0 1 0 0 0 - 0 0 2 0 2 1 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 1 0
Uroctea sp	0 0 0 1 0 0 0 0 0 0 - - 1 0 0 0 0 0 0 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 0 - - 0 1 0 1 0 0 0 - 0 0 2 0 1 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 0 0
Gnaphosidae *sp*	0 0 0 0 0 2 1 0 0 0 - - 1 0 0 2 5 0 1 0 0 0 0 - - 0 0 0 - 0 1 - 0 0 1 2 1 0 1 0 0 0 0 1 1 2 0 2 0 1 0 0 - - 0 0 - 0 - - 0 0 - 0 - - 0 0 1 0
Palpimanus sp	0 0 0 1 0 0 1 0 2 1 3 0 1 3 1 0 0 0 0 1 1 1 0 - - 0 1 1 2 1 1 - 0 0 1 0 0 0 1 2 a a 0 0 - 0 0 0 0 2 1 0 - - 0 0 - 1 0 0 0 1 0 0 0 - 1 0 0 0
Colopea sp	0 0 0 1 0 0 1 1 2 1 2 0 1 0 1 0 0 0 0 1 0 1 0 - - 0 0 1 0 1 0 0 0 0 1 0 1 0 1 2 a 0 0 0 - 0 0 0 0 2 1 0 - - 0 0 - 0 - - 0 1 0 0 - - 1 0 0 0
Huttonia sp	0 0 0 1 0 0 1 0 1 0 - - 0 0 1 0 0 0 0 0 0 0 0 - - 0 0 1 0 3 1 - 0 0 1 2 1 0 1 b 1 0 0 0 - 0 0 a 0 2 1 0 - - 0 0 - 1 1 1 0 1 1 0 1 0 1 0 0 0
Aotearoa magna	1 2 0 0 0 0 1 0 1 1 1 1 0 1 1 0 1 0 1 1 ? 0 1 0 - 0 0 1 1 1 0 1 0 0 0 - - 0 1 b 1 0 0 0 - 0 ? ? 0 ? 1 1 0 0 1 1 1 1 1 0 0 1 0 0 1 1 1 0 0 0
Mesarchaea bellavista	1 2 1 - - - 1 0 b 1 1 1 0 1 1 0 1 0 1 1 0 0 1 1 1 0 0 1 1 1 0 1 0 0 0 - - 0 1 b 1 0 0 0 - 0 ? ? 0 ? 1 1 0 0 1 1 1 1 1 0 0 1 1 0 1 1 1 0 0 0
Mecysmauchenius segmentatus	0 0 1 - - - 1 0 1 1 1 1 0 1 1 0 1 0 1 1 1 0 1 0 - 0 0 1 1 1 0 1 0 0 0 - - 0 1 b 1 0 0 0 - 0 0 a 0 2 1 1 0 0 1 1 1 1 1 0 0 1 2 0 1 1 1 0 0 0
Chilarchaea quellon	0 0 1 - - - 1 0 1 1 1 1 0 1 1 0 1 0 1 1 0 0 1 0 - 0 0 1 1 1 0 1 0 0 0 - - 0 1 b 1 0 0 0 - 0 0 a 0 1 1 1 0 1 1 1 1 1 1 1 0 0 1 2 0 b - 1 0 0 0
Zearchaea sp	2 2 0 0 0 0 1 0 1 1 1 1 0 1 1 0 b 0 1 1 0 0 1 0 - 0 0 1 1 1 0 1 0 0 0 - - 0 1 b 1 0 0 0 - 0 0 a 0 2 1 1 0 0 1 1 1 1 0 0 0 1 0 0 0 0 1 0 0 0
Eriauchenius lavatenda	2 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 1 1 1 0 1 1 1 0 1 1 1 1 1 - 1 1 1 2 1 1 1 1 1 0 0 0 - 0 1 a 0 2 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Eriauchenius jeanneli	2 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 0 0 1 1 1 1 1 - 1 1 1 2 1 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Eriauchenius legendrei	2 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 1 0 1 1 1 1 1 - 1 1 1 2 ? 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Eriauchenius workmani	1 0 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 1 1 1 0 1 1 1 0 1 1 1 1 1 - 1 1 1 2 1 1 1 1 1 0 0 0 - 0 1 a 0 2 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Eriauchenius bourgini	1 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 0 0 1 1 1 1 1 - 1 1 1 2 1 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Afrarchaea sp.	1 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 1 0 1 1 1 1 1 - 1 1 1 1 1 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Afrarchaea woodae	1 1 0 1 1 1 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 1 0 1 1 1 1 1 - 1 1 1 1 0 1 1 1 1 0 0 0 - 0 1 a 0 2 1 1 0 0 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Austrarchaea nodosa	1 0 0 1 1 0 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 0 0 1 1 1 1 1 - 1 1 1 2 0 1 1 1 1 0 0 0 - 0 1 a 0 2 1 1 1 1 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Austrarchaea daviesae	1 0 0 1 1 0 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 0 0 1 1 1 1 1 - 1 1 1 2 1 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 1 1 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Austrarchaea mainae	0 0 0 1 1 0 1 0 2 1 0 1 0 2 1 1 2 1 0 1 1 0 1 1 0 0 1 1 1 1 1 - 1 1 1 2 0 1 1 1 1 0 0 0 - 0 ? ? ? ? 1 1 1 1 1 0 - 1 1 1 0 1 0 1 1 0 1 1 0 0
Archaea paradoxa	0 0 0 1 1 0 ? 0 2 1 0 1 0 0 1 ? 2 1 0 1 1 ? 1 1 1 1 0 1 1 1 ? ? 1 1 1 ? ? 1 1 ? 1 0 0 0 - 0 ? ? ? ? 1 0 - - 1 0 - 1 1 1 ? 1 0 0 1 1 1 1 0 0
Burmesarchaea grimaldii	0 0 0 1 1 0 ? 0 2 1 0 1 0 0 1 ? ? ? 0 1 1 ? 1 1 1 1 0 ? ? ? ? ? 1 ? ? ? ? 1 1 ? 1 0 0 0 - 0 ? ? ? ? 1 0 - - 1 0 - 1 1 ? ? 1 ? 0 1 0 ? ? 0 0
Myrmecarchaea sp	0 0 0 1 1 0 ? 0 1 1 ? 1 0 0 ? ? ? ? 0 1 ? ? 1 1 1 1 0 ? ? ? ? ? 0 1 1 ? ? 1 1 ? ? ? 0 ? ? ? ? ? ? ? ? 1 0 - - ? 0 - 1 ? ? ? ? ? 0 1 1 ? ? 0 0
Baltarchaea conica	1 0 0 1 1 0 ? 0 2 1 1 1 0 0 ? ? 2 ? 0 1 1 ? 1 1 1 1 0 ? ? ? ? ? 0 1 ? ? ? 1 1 ? ? ? 0 ? ? ? ? ? ? ? ? 1 0 - - 1 0 - 1 ? ? ? 1 0 0 1 ? ? ? 0 0
Patarchaea muralis	? ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 1 ? 1 ? ? ? ? ? ? ? 0 ? 1 1 ? ? 1 ? 1 0 ? ? ? ? ? ? ? ? ? 1 0 - - 1 0 - 1 1 ? ? 1 1 0 1 ? 1 ? 0 0

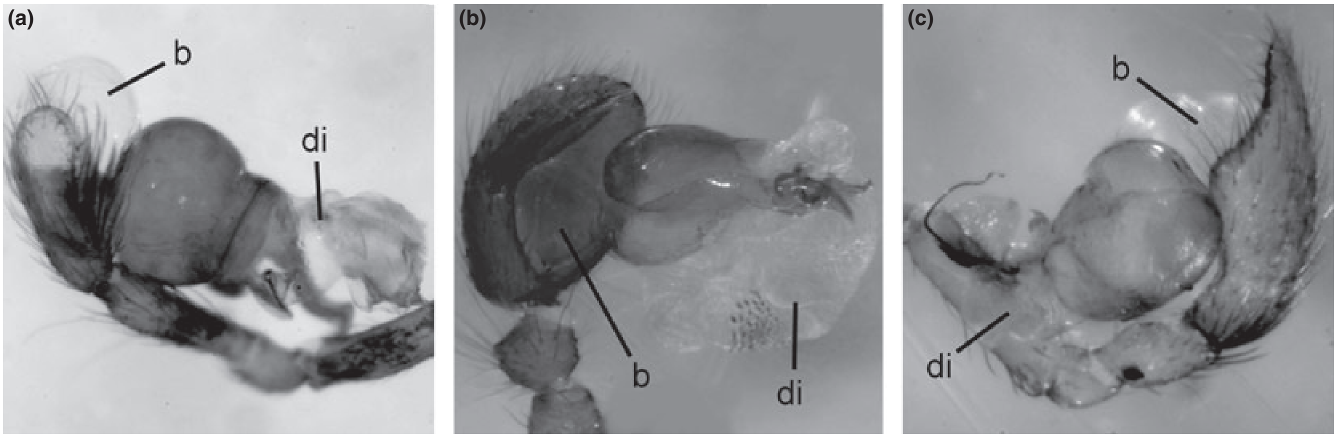

Fig. 9. Expanded male palp, left. (a) *Eriauchenius legendrei*, prolateral (right palp, image flipped to appear left). (b) *Colopea* sp., prolateral. (c) *Zearchaea* sp., retrolateral. "di" showing distal expansion, "b" showing basal expansion.

stenochilids and which have evolved independently in mimetids and pararchaeids. In the taxa in this study, the most favourable likelihood character reconstruction finds that the presence of cheliceral stridulatory ridges (character 62) is a synapomorphy for Palpimanoidea, which evolved independently in *Loxosceles* and *Hickmania*, whereas in the parsimony reconstruction it is ambiguous whether this trait evolved independently or was lost independently. A gland mound is present on the chelicerae in all Palpimanoidea (character 67), which has also evolved independently in holarchaeids. Within Palpimanoidea (also evolved independently in some Araneoidea taxa) there is a cheliceral diastema (character 72), and this was scored as present in *Palpimanus* and *Colopea* because of the presence of a sclerotized rod running between the chelicerae and mouthparts. An interesting Palpimanoidea synapomorphy involves the wrinkle pattern observed in the abdomen

Appendix 2 *continued*

	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
	7 7 7 7 7 7 7 7 7 8 8 8 8 8 8 8 8 8 8 9 9 9 9 9 9 9 9 9 9 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2
Character	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 1 1 1 1 1 1 1 1 0 1 2 3 4 5 6
Hypochilus pococki	0 0 0 - 0 1 0 1 0 2 0 - 0 0 0 0 - 0 1 0 1 0 0 - - 0 - - 0 0 1 1 1 ? ? 1 0 0 0 0 - 0 0 0 1 0 0 0 - 0 1 0 0 0 - 0
Hickmania troglodytes	0 0 0 - 0 1 0 1 0 0 0 - 0 0 0 0 - 0 1 0 1 0 0 - - 1 0 1 0 0 0 - 0 ? ? 0 - 0 0 0 - 0 0 0 1 0 0 1 1 0 1 0 0 1 0 1
Lycosidae *sp*	0 0 0 - 2 0 0 ? 0 0 0 - 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 0 0 0 - - - - - 0 0 1 1 0 1
Araneus sp	0 0 0 - 2 0 0 1 0 1 0 - 0 1 0 0 - 0 1 0 1 1 0 - - 0 - - 0 1 1 0 1 0 0 1 2 0 0 0 - 0 0 1 0 - - - - - 1 1 0 1 1 1
Badumna longinqua	0 0 0 - 2 0 0 0 0 0 0 - 0 1 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 1 1 1 ? ? 0 - 0 0 1 3 0 0 0 1 1 0 1 0 1 1 0 1 1 0 1
Dysdera sp	0 0 0 - 2 1 0 0 0 1 0 - 0 0 0 1 0 0 0 - 1 0 1 0 0 0 - - 1 0 0 - 1 ? ? 0 - 0 0 0 - 0 0 0 0 - - - - - 0 0 0 0 2 0
Holarchaea sp	0 1 0 - 2 0 0 0 0 1 0 - 0 0 0 0 - 0 1 0 0 1 0 - - 0 - - 0 1 0 - 0 ? ? 0 - 0 1 0 - 0 0 0 0 - - - - - 0 1 1 1 0 1
Kukulcania hibernalis	1 0 0 - 1 1 0 1 0 1 0 - 0 0 0 0 - 0 1 0 1 0 0 - - 0 - - 1 0 0 - 0 1 ? 0 - 0 0 0 - 0 0 0 1 1 1 1 1 1 0 0 0 0 0 0
Loxosceles sp	1 0 0 - 2 0 0 1 0 1 0 - 0 0 0 0 - 1 1 0 1 0 0 - - 0 - - 1 0 0 - 0 ? ? 0 - 0 0 0 - 0 0 0 0 - - - - - 0 0 1 0 2 0
Mimetus sp	1 1 0 - 2 0 0 1 0 1 0 - 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 1 1 0 1 ? ? 1 2 0 0 0 - 0 0 0 0 - - - - - 0 1 0 1 1 1
Pararchaeidae *sp*	0 1 0 - 2 0 0 1 0 1 1 2 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 1 1 1 ? ? 1 2 0 0 0 - 0 0 0 0 - - - - - 0 1 1 1 2 1
Stegodyphus sp	0 0 0 - 2 0 0 1 0 1 0 - 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 1 1 0 ? ? 0 - 0 0 0 - 0 0 0 1 1 0 0 - 0 1 0 0 1 0 1
Uroctea sp	0 0 0 - 2 0 0 1 0 1 0 - 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 1 0 1 0 0 0 - 0 0 0 - 0 0 0 0 - - - - - 0 0 0 1 2 1
Gnaphosidae *sp*	0 0 0 - 2 0 1 1 0 a 0 - 0 0 0 0 - 0 1 0 1 1 0 - - 0 - - 0 0 0 - 1 ? ? 0 - 0 0 1 0 0 0 0 0 - - - - - 1 0 1 1 0 1
Palpimanus sp	0 1 0 - 2 0 0 0 1 1 1 2 0 1 0 1 1 1 0 - 0 0 0 - - 1 1 1 ? 0 ? ? ? 1 1 0 - 0 0 0 - 0 0 1 0 - - - - - 0 0 1 1 2 1
Colopea sp	0 1 0 - 2 0 0 0 1 0 1 3 0 1 0 1 1 1 0 - 2 0 0 - - 1 1 0 0 0 1 0 0 ? ? 0 - 0 0 0 - 0 0 1 0 - - - - - 0 0 1 1 2 1
Huttonia sp	0 1 0 - 2 0 0 0 0 1 0 - 0 1 0 1 1 1 1 0 0 0 0 - - 1 1 1 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 0 1 0 - - - - - 0 0 1 1 2 1
Aotearoa magna	0 1 0 - 2 0 0 ? 1 ? 0 - 0 ? 0 0 - 1 1 1 ? 0 0 - - 1 1 1 0 0 1 0 1 ? ? 0 - 0 0 1 1 1 0 1 0 - - - - - ? ? 1 ? ? ?
Mesarchaea bellavista	0 1 0 - 2 0 0 1 1 ? 0 - 0 ? 0 0 - 1 ? ? ? 0 ? ? ? ? ? ? ? 0 0 1 0 ? ? ? 0 - 0 0 1 2 1 0 1 0 - - - - - ? ? 1 ? ? ?
Mecysmauchenius segmentatus	0 1 0 - 2 0 0 1 1 0 0 - 0 0 0 0 - 1 1 1 2 0 0 - - 1 0 1 0 0 1 0 ? 1 ? 1 0 0 0 1 1 1 0 1 0 - - - - - 0 1 1 1 2 1
Chilarchaea quellon	0 1 0 - 2 0 0 1 1 0 0 - 0 1 0 0 - 1 1 - 2 0 0 - - 1 0 1 0 0 0 - 0 ? ? 1 1 0 0 1 1 1 0 1 0 - - - - - 0 0 1 1 2 1
Zearchaea sp	0 1 0 - 2 0 0 1 1 0 0 - 0 1 0 0 - 1 1 1 2 0 0 - - 1 1 1 0 0 1 0 1 ? ? 0 - 1 0 1 1 1 0 1 0 - - - - - 0 1 1 1 2 1
Eriauchenius lavatenda	0 1 0 - 2 1 0 0 0 0 1 1 1 1 1 1 0 1 0 - 1 0 1 1 0 0 - - 0 0 1 0 1 ? ? 0 - 0 1 0 - 0 1 1 0 - - - - - 0 1 1 1 0 1
Eriauchenius jeanneli	0 1 0 - 2 1 0 0 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 1 1 0 0 - - 0 0 1 0 1 ? ? 0 - 0 1 0 - 0 1 1 0 - - - - - ? ? 1 ? ? ?
Eriauchenius legendrei	0 1 0 - 2 1 0 0 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 1 0 0 0 - - 0 0 1 0 1 ? ? 0 - 1 1 0 - 0 1 1 0 - - - - - ? ? 1 ? ? ?
Eriauchenius workmani	0 1 1 1 2 1 0 0 0 0 1 1 1 1 1 1 0 0 0 - 1 0 1 1 0 0 - - 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 1 1 0 - - - - - 0 1 1 1 0 1
Eriauchenius bourgini	0 1 0 - 2 1 0 0 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 1 1 0 0 - - 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 0 1 0 - - - - - ? ? 1 ? ? ?
Afrarchaea "sp.	0 1 0 - 2 1 0 0 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 1 1 1 0 - - 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 1 1 0 - - - - - ? ? 1 ? ? ?
Afrarchaea woodae	0 1 0 - 2 1 0 0 0 0 1 1 1 1 1 1 0 0 0 - 1 0 1 1 1 0 - - 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 1 1 0 - - - - - 0 1 1 1 2 1
Austrarchaea nodosa	0 1 1 0 2 1 1 1 0 0 1 1 1 1 1 1 0 0 0 - 1 0 0 - - 1 0 0 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 1 1 0 - - - - - 0 1 1 1 0 1
Austrarchaea daviesae	0 1 1 0 2 1 1 ? 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 0 - - 1 0 0 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 1 1 0 - - - - - ? ? 1 ? ? ?
Austrarchaea mainae	0 1 1 0 2 1 1 ? 0 ? 1 1 1 ? 1 1 0 0 0 - 1 0 0 - - 1 0 0 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 0 1 0 - - - - - ? ? 1 ? ? ?
Archaea paradoxa	0 1 0 - ? ? 1 ? 0 ? 1 1 1 ? 1 0 - 1 0 - ? 0 ? ? ? ? ? ? ? 0 0 1 0 1 ? ? 0 - 0 0 0 - 0 0 1 0 - - - - - ? ? ? ? ? ?
Burmesarchaea grimaldii	0 1 0 - ? ? ? ? 0 ? ? ? 1 ? 1 0 - ? ? ? ? ? ? ? ? ? ? ? ? 0 0 1 0 ? ? ? 0 - 0 0 0 - 0 1 ? 0 - - - - - ? ? ? ? ? ?
Myrmecarchaea sp	0 1 0 - ? ? ? ? 0 ? ? ? 1 ? 1 ? 0 - - - - - ? ? ? ? ? ?
Baltarchaea conica	0 1 1 a ? ? ? ? 0 ? ? ? 1 ? 1 ? ? ? ? ? ? 0 ? 0 - - - - - ? ? ? ? ? ?
Patarchaea muralis	0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 0 - ? 1 0 ? ? ? ? ? ? ? ? 0 ? ? ? ? ? ? 0 - ? ? 1 1 ? ? ? 0 - - - - - ? ? ? ? ? ?

cuticle after being critically point dried (character 84, Fig. 7c). In Palpimanoidea taxa, although with some taxa scored as ''unknown'' and lost in *Mecysmauchenius*, the cuticle has a distinctive pattern (also compare figs 44, 100, 316 and 331 with figs 226 and 365 of Platnick and Forster, 1984); this evolved independently in *Badumna* and *Araneus*. Another shared characteristic of Palpimanoidea (although lost in most extant archaeids) is the presence of picks on the palpal femur (character 88), which also occurs independently in *Loxosceles* sp. Palpimanoidea taxa (with the exception of the African/Madagascar archaeids) and *Hickmania troglodytes* have large membranous sacs originating from the bursa, or sperm storage organ, in the female genitalia (character 96). As this trait does not appear in the Entelegynae clade, this feature either evolved twice independently or evolved once and was then lost in the Entelegynae, as found ambiguous in the parsimony character reconstruction. In the likelihood reconstruction the favoured scenario is independent evolution in Palpimanoidea and *Hickmania*. An important morphological discovery is the finding that the distal membranous section of the male palpal bulb expands (character 114, Fig. 9) in all Palpimanoidea. The male palp serves as secondary genitalia in spiders; in Entelegynae only the basal parts of the bulb expand during copulation. Distal expansion of the palp bulb may be exclusive to the Palpimanoidea and was even observed in a fossilized *Archaea paradoxa* specimen. This character state was also scored as present in *Araneus* sp. even though the expansion involves movable ''joints'' within sclerotized structures rather than an entire ballooning out of the distal palpal membranes, which is a synapomorphy for Palpimanoidea.

There are several other notable characters within Palpimanoidea that are worth mentioning for diagnostic purposes. Palpimanoidea taxa have either tuberculate (or bumpy) or scaly cuticle (character 9) on the carapace. The transition from tuberculate to scale or vice versa has occurred several times within the Palpimanoidea. A synapomorphy for the non-mecysmaucheniid Palpimanoidea is that the anterior median eyes (AME) are larger than the other eyes (character 4), a trait that has independently evolved in several non-Palpimanoidea taxa. Another synapomorphy uniting non-mecysmaucheniid Palpimanoidea is the presence of modified spatulate hairs, termed scopulae, which are found on the inside surface of leg I and sometimes leg II (character 35). This character is also evolved independently in Gnaphosidae. Within the Palpimanoidea, peg-teeth also occur on the retrolateral margin of the chelicerae, close to the location where the fang closes (character 59, Fig. 7f), whereas in non-Palpimanoidea taxa the peg-teeth occur only on the promargin. With the exception of archaeids and huttoniids, the posterior row of spinnerets is greatly reduced (character 79). *Palpimanus*, *Colopea*, and archaeids are heavily sclerotized around the anterior portion of the abdomen, while this does not occur in *Huttonia* and the mecysmaucheniids (character 81). The presence of a brush of hairs on the palp tarsus (character 86) occurs in several members of the Palpimanoidea, as well as independently in *Dysdera* sp.

Appendix 4: Archaeidae synapomorphies

Character reconstructions were performed using both parsimony and likelihood methods, and the results were similar (meaning the most favourable likelihood reconstruction was the same as the parsimony reconstruction) unless otherwise stated. Some characters that are synapomorphies for all archaeids, extant and fossil, include: the anterior median eyes are on a ridge (character 5); the seam that fuses the edges of the carapace to form a foramen around the base of the chelicerae is rebordered or thickened, lost in *Baltarchaea conica* (character 11); the sclerite between the chelicerae bases is triangular (character 17, Fig. 5a), and beneath this there is an additional long, narrow sclerite (character 18, Fig. 5A); the labium has a narrow v-shaped notch at the distal edge (character 21—also evolved independently in other taxa); the cephalic area is raised at least the length of the carapace (character 23—also evolved independently in other taxa, Fig. 1e,g,h); there is a constriction in the ''neck'' (character 24—also evolved independently in *Mesarchaea*, Fig. 1e,g,h); the parsimony character reconstruction found that the presence of a membranous ring around the basal portion of the tarsi (character 29) was ambiguous and could either be an archaeid synapomorphy (that evolved independently in mecysmaucheniids) or alternatively and in agreement with the most favourable likelihood reconstruction, that this trait was a synapomorphy for Palpimanoidea that was lost twice independently; femur IV has a distinctive bend (character 33, missing in some fossil archaeids), which is a synapomorphy for archaeids in the most favourable likelihood reconstruction, yet it is ambiguous in the parsimony reconstruction whether this trait evolved once in the family and was lost in some fossils, or whether it evolved twice within the family; femora I–IV have a small, dorsal bump (character 34); the patella–tibia joint of leg IV is hyperextended (character 38—also evolved independently in *Holarchaea*); there is a constriction immediately preceding the cheliceral bases (character 55—also evolved independently in mecysmaucheniids and *Holarchaea*); there are only two peg teeth in the first row (character 60—also occurs independently in *Huttonia*), although in the parsimony reconstruction it is ambiguous whether this is a synapomorphy for the Palpimanoidea that has been lost in some members, whereas the likelihood reconstruction suggests this trait evolved independently in archaeids and huttoniids; there is a deep depression adjacent to the cheliceral gland mound (character 68); in females the dorsal and ventral sclerites that surround the anterior of abdomen are separate (character 82)—although in the likelihood and parsimony reconstructions it is equally favourable (and ambiguous) whether this character evolved only in archaeids, or in archaeids + stenochilids and then later changed states in stenochilids; there are folds in the abdomen (character 83, Fig. 1e), which are less obvious in the extant archaeids, but still visible, especially in a hungry individual; the spinnerets arise from a conical projection (character 85).

Appendix 5: Extant Archaeidae synapomorphies

Character reconstructions were performed using both parsimony and likelihood methods, and the results were similar (meaning the most favourable likelihood reconstruction was the same as the parsimony reconstruction) unless otherwise stated. Some of the following characters were not scored for the fossil archaeids because these features were too small to observe in amber specimens. For this reason and only when noted, some of these characters may turn out to be true for both the extant and the fossil archaeids. All extant archaeids have the synapomorphy of a tubercle on the posterior edge of their sternum (character 14). The chilum is divided (character 16, Fig. 5a); this character was unable to be scored for fossil archaeids. The posterior edge of the carapace is flattened in extant archaeids rather than tapering off (character 27—also evolved independently in *Palpimanus*, Fig. 7b). The extant archaeids have serrate accessory claw setae (character 47), but again this trait is not scored for fossil archaeids. Extant archaeids, unlike their extinct relatives, have a spine or protuberance on the anterior surface of their chelicerae (character 52). This character was also reported in the fossil *Burmesarchaea grimaldii* but our observations did not confirm this observation. The distal portion of the chelicerae is curved towards the posterior and is a synapomorphy for extant archaeids (character 64). In extant archaeids the posterior respiratory system consists of a pair of tracheae (character 76), unlike the single opening seen in most Araneomorphae. This character is unable to be scored in the fossil archaeids, and could be a synapomorphy for the entire family. Extant archaeids have a brush of hairs that occurs on the palp tarsi (character 86), which evolved independently in extant archaeids (although on the prolateral side) and other Palpimanoidea taxa (occurring on the retrolateral side)

in the most favourable likelihood reconstruction, whereas in the parsimony reconstruction, evolution of this trait is ambiguous. This brush of hairs has been observed to interact with the stridulatory file on the chelicerae (Forster and Platnick, 1984; Wood, 2008) to produce courtship vibrations, and in the fossil archaeids stridulatory picks instead likely interact with the stridulatory file. Unlike the fossil archaeids (although the only fossil that could be scored for this character was *Archaea paradoxa*) and other Palpimanoidea, the extant archaeids do not have picks on palpal femur (character 88—although these do occur in *Eriauchenius gracilicollis*, an extant species not included in this study). The major ampullate gland spigot (MAP) field on the ALS is separated by a furrow in extant archaeids (character 122). This character evolved independently in other taxa in our study, and is also unable to be scored in the fossil archaeids, so this trait may be a synapomorphy of the family. In most extant archaeids the minor ampullate gland spigot (mAP) on the PMS is median to anterior (character 125—also occurs in other taxa), although this character is scored as "unknown" in the fossil archaeids. A final character worthy of discussion involves the length of the endites (the mouthparts), which are greatly extended in the fossil archaeids (character 26), whereas the extant archaeids have shorter endites comparable with those of other spiders. In the parsimony reconstruction of this character it is ambiguous whether this trait evolved once in the family and then was lost in the extant archaeids, or evolved twice independently in the fossil archaeids. The likelihood reconstruction favours the scenario where greatly extended endites evolved once in archaeids and then were lost in the extant archaeids.

Appendix 6: Placement of the fossil *Lacunauchenius speciosus*

The Burmese amber fossil (Cretaceous, Penney, 2003) *Lacunauchenius speciosus* Wunderlich, 2008, is an enigmatic species with an elevated and modified carapace, and is known from only one male specimen. This fossil was ultimately removed from this study because it is poorly preserved in cloudy amber, making it difficult to distinguish whether assigned character states were real or instead artefacts of preservation. This specimen very likely belongs to the Palpimanoidea based on the presence of peg teeth that also occur on the fang retromargin, having both tubercles and scales for the carapace texture, having a foramen surrounding the chelicerae bases, a raised carapace and a brush of hairs on the third metatarsus. This specimen has a grossly elevated carapace similar to the archaeids and mecysmaucheniids. This specimen has several traits that are archaeid synapomorphies, having anterior median eyes that are on a ridge (character 5) and the presence of a bend in femur IV (character 33), yet the legs and carapace of this specimen are distorted, so the presence of these traits may be due in fact to poor preservation. On the other hand, this specimen also has greatly elongated hairs on the inner margins of the chelicerae, very similar to those that serve as "trigger hairs" in the mecysmaucheniids. As these long hairs are only known from the spider families that seem capable of locking their chelicerae open (the mecysmaucheniids and pararchaeids), the presence of these hairs argues that this specimen may also possess this mechanism, possibly related to the mecysmaucheniids. Yet, because the specimen is poorly preserved and because it is a fossil, it could not be scored for additional mecysmaucheniid traits, such as the shape of the sclerite at the base of the chelicerae (character 17) and the shape of the tarsal organ (character 31 and 32), a microscopic sensory organ which can only be viewed using a scanning electron microscope. Furthermore, the posterior row of spinnerets is not reduced as is found in the mecysmaucheniids (character 79), and the abdomen does not have characteristic folds found in the archaeids (character 83). This enigmatic fossil is currently considered a monotypic archaeid genus (Wunderlich, 2008), but it is also possible it could be a new Palpimanoidea family, or a new genus of mecysmaucheniid. Caution should be used regarding the phylogenetic placement of this taxon until more fossil specimens are discovered.